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MIOCENE HERPETOFAUNAS FROM THE CENTRAL GULF COAST USA: THEIR PALEOECOLOGY, BIOGEOGRAPHY, AND BIOSTRATIGRAPHY

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Geology and Geophysics

by
Michael John Williams
B.S., Louisiana State University, 2002
December 2009

DEDICATION

This dissertation is dedicated, first and foremost, to my wife, Beth, two kids, Marella and Isabella, and dad, all of whom felt the stress of long hours of research and writing and many days of "Daddy" not being available. Their patience, encouragement, and understanding are appreciated much more than words can convey.

ACKNOWLEDGEMENTS

Many people and institutions were instrumental in the completion of this dissertation. My advisor Dr. Schiebout cannot be thanked enough, as she was available day and night to answer questions, review drafts, and offer words of encouragement. My committee members, Drs. Ellwood, Warny, and Hanor and Dean's Representative, Dr. Tague, were invaluable for their critique and suggestions, which greatly improved this dissertation. I would like to thank Dr. Tague I would like to extend a tremendous thanks to Mary Lee Eggart from the Department of Geography and Anthropology for beautifying many of the figures.

A very special thank you to Dr. Suyin Ting from the LSU Museum of Natural Science, who taught me very important paleontological field and laboratory techniques and processed, picked, and prepared many of the catalogued specimens from Fort Polk. I thank Ruth Hubert for her dedication as a long-time volunteer in the vertebrate paleontology laboratory and her thoughtful conversations. Her daughter Cathy Lamb (Fox) also dedicated time picking fossil microvertebrates. The Hubert Charitable Foundation has provided support for the vertebrate paleontological laboratory during Fort Polk and TunicaHills/Kerry work. Kerry Dicharry discovered the TunicaHills/Kerry site. Thank you to her mother Kathleen MacDonald for all her help in the laboratory and field. Thank you to volunteer and friend Bill Lee for his dedication to, and passion for, Louisiana paleontology and to the many student workers and volunteers, such as Ray Wilhite, Grant Boardman, Julie Hill, Mark Hagge, Barry and Ellen Meyer, Dr. John Wrenn, Lorene Smith and Brandon Kilbourne, who also participated in field and/or laboratory work. The Department of Geology and Geophysics at LSU provided teaching assistantships. The Museum of Natural Science at LSU provided employment as a curatorial assistant and the long-term loan of modern osteological specimens. Thanks to Southern Methodist University for the long-term

loan of early Miocene herpetological specimens from east Texas. Thank you to the staff at the Fort Polk environmental learning center, especially Jim Grafton and Bob Hayes, who spent many hours with researchers and students from LSU prospecting sites for fossils and bagging matrix for underwater sieving. Thank you to Giar-Ann Kung from the Natural History Museum of Los Angeles County, for her help and guidance with the scanning electron microscope. Thanks to colleagues in the vertebrate paleontology section of the Natural History Museum of Los Angeles County for their helpful suggestions. I thank the University of Nebraska State Museum and the Florida Museum of Natural History who permitted access to specimens and reprints while visiting. Most importantly, I need to thank my family, for their understanding, patience, and urging to push on and finish up. This work was supported in part by a Sigma Xi Grant-in-aid of Research.

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ABBREVIATIONS AND ACRONYMS

Anterior Truck Vertebrae ATV
Louisiana State University LSU
Louisiana State University Museum of Geoscience a division of LSU Museum of Natural Science LSUMG
Middle Miocene Climatic Optimum MMCO
Middle Trunk Vertebrae MTV
Million years ago Ma
Posterior Trunk Vertebrae PTV
Scanning Electron Micrograph SEM
Shuler Museum of Paleontology Southern Methodist University SMPSMU
Species sp.
University of Florida UF
University of Michigan Museum of Paleontology UMMP
University of Nebraska State Museum UNSM

ABSTRACT

The late Barstovian Fort Polk herpetofauna represents the most diverse herpetofauna on the Gulf Coast, USA, and includes 15 genera from ten families. The herpetofaunal composition of Fort Polk and Miocene east Texas localities is similar enough to Great Plains localities that they are all considered to be one biogeographical province during the Barstovian. The use of ternary diagrams, ratios of herpetological elements to kg matrix screened, and natricine-colubrine indices, has allowed determining the wetness of the Fort Polk sites. Development of a composite stratigraphic section for North American fossil snakes has allowed recognition of two extinctions of fossil snakes during the Miocene. North American and European Miocene snake faunas display a replacement of boids by colubrids in the Early to Middle Miocene and Late Oligocene, respectively. European fossil snake data show a decrease in colubrid numbers from the Early to Middle Miocene.

CHAPTER 1: INTRODUCTION

Statement of the Problem

Prior to the discovery by researchers from Louisiana State University of fossil microvertebrate exposures in western Louisiana (Schiebout, 1997; Schiebout and Ting, 2001; Schiebout *et al*., 2002; Schiebout *et al*., 2004 and Williams and Schiebout, 2003), Miocene central Gulf Coast Miocene fossil herpetofaunal data were very scanty, though Miocene herpetofaunas are well-documented in the high plains. Such scanty data are due in part to a lack of Gulf Coast Miocene exposures yielding vertebrate microfaunas. Compared to similar-aged localities in the High Plains, the known Miocene Gulf Coast localities have not yet yielded large numbers of isolated amphibian and reptile fossils. Before the 1993 discovery of the Middle Miocene Fort Polk sites in west central Louisiana (Schiebout, 1997; Schiebout and Ting, 2001; Schiebout *et al*., 2002; Schiebout *et al*., 2004 and Williams and Schiebout, 2003), there were no known Miocene herpetofaunas between the Early Miocene Toledo Bend, Texas locality (Albright, 1991; Albright, 1994) and the Middle Miocene Willacoochee Creek locality on the eastern Florida panhandle (Bryant, 1991; Figure 1-1).

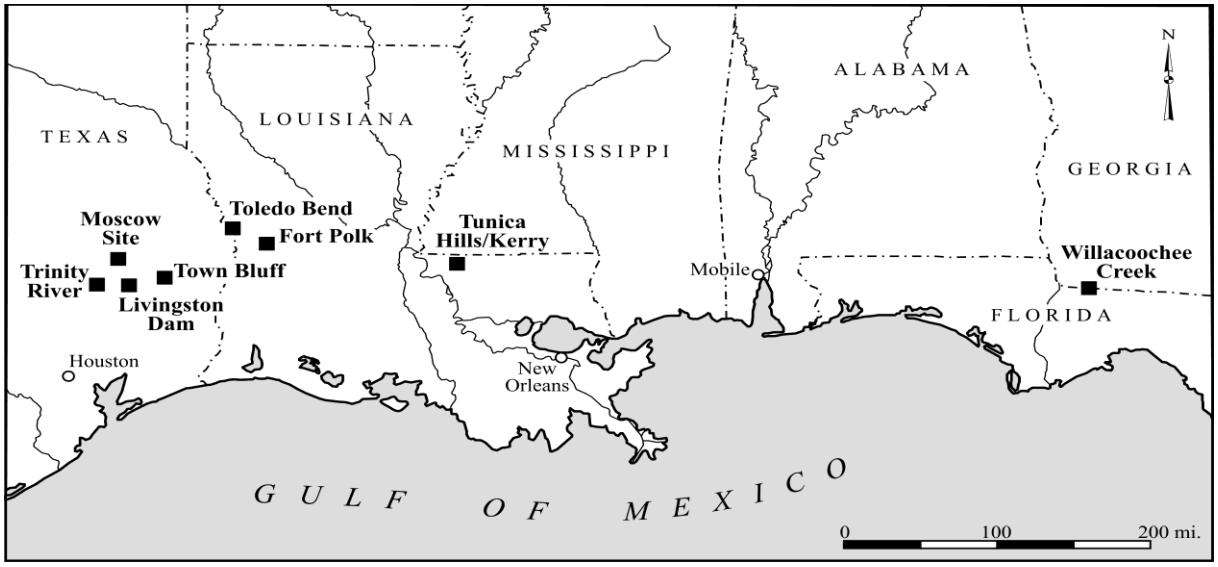

Figure 1-1. Map of central Gulf Coast Neogene herpetofaunal-bearing localities.

Much of the early work on Neogene vertebrate fossil localities focused on the large mammal remains present, with little attention paid to vertebrate microfossils. The advent of wet sieving techniques developed by Hibbard (1949) and recognition of the importance of vertebrate microfaunas by the 1950's, led to increased knowledge of Neogene herpetofaunas from Florida, California, and the High Plains.

This dissertation encompasses description of herpetofaunas from the Fort Polk and TunicaHills/Kerry sites on the central Gulf Coast, which were collected mainly using wet sieving techniques and includes collecting of data on Miocene herpetological sites worldwide from the literature, to place the Gulf Coastal sites in context. The documentation and analysis of these herpetofaunas has facilitated answering paleoenvironmental, paleoclimatological, biogeographical, and evolutionary questions. Some of the questions this research sought to answer are: 1) were changes in global climate the reason for the proliferation of modern colubrid snake taxa in North America and Europe; 2) do Miocene ophidian faunas from Gulf Coastal eastern Texas and Louisiana display the same pattern of caenophidian replacing henophidian snakes in the early to middle Miocene as seen elsewhere 3) can plotting taxon's geographic ranges during each North American Land Mammal Age identify range expansions, contractions or endemism; 4) can paleoenvironmental inferences using fossil amphibians and reptiles be quantified through the use of paleoenvironmental indices?

Miocene herpetofaunas evolved during a time of tremendous climatic and biotic change. Significant events in earth history occurred during this epoch including the spread of C3 and C4 grasslands across parts of North America and Europe (Axelrod, 1985; Cerling *et al*., 1993; Wang *et al*., 1994; Retallack, 1997; MacFadden, 2000; Passey *et al*., 2002; Stromberg, 2002**)**, the rise of many hypsodont land mammal lineages **(**Wang *et al*., 1994; Retallack, 1997; MacFadden,

1991, 2000; Stromberg, 2002**),** and the warmest period in the Neogene, namely, the Middle Miocene climatic optimum (MMCO) (Figure 1-2). Miocene herpetofaunas also underwent significant changes. There is a well-documented transition among snakes in North America and Europe from Early Miocene boid-dominated ophidian faunas to late Miocene faunas dominated by modern colubrid, viperid, and elapid taxa (Holman, 1976, 1976B, 2002; Ivanov, 2000, 2002; Parmley and Holman, 1995, 2002; Rage, 1988, 2005; Szyndlar and Schleich, 1993; Whistler and Wright, 1989). Finally, the diversification of modern frog genera occurred during the Miocene (Holman, 2003).

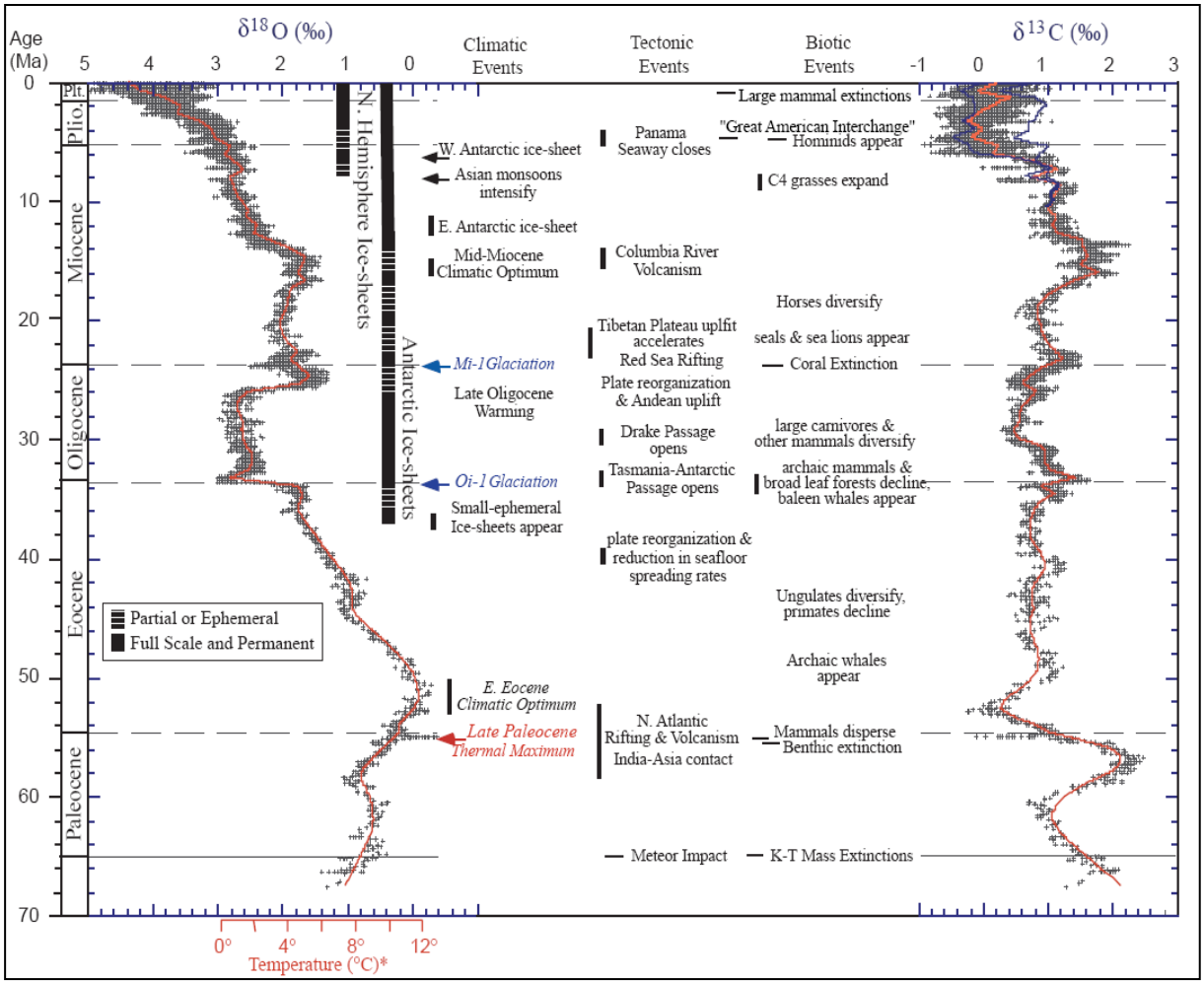

Figure 1-2. Graph of global $\delta^{18}O$ and $\delta^{13}C$ values for the Cenozoic, including pertinent climatic, tectonic, and biotic events. Modified from Zachos et al. (2001).

Earth's temperature warmed significantly during the Late Oligocene, decreasing the size of the Antarctic ice sheets that were present throughout the Oligocene (Zachos et al., 2001; Figure 1-2). Although there was a slight cooling trend from early to middle Miocene times, average global temperatures remained warm through the Middle Miocene climatic optimum, which occurred between 17 and 15 Ma (Zachos et al., 2001; Figure 1-2). After 15 Ma, the climate grew increasingly cooler as the east Antarctic ice sheet formed and increased in volume. This cooling trend continued until the Late Miocene and Early Pliocene, when two small and separate increases in temperature occurred (Zachos et al., 2001; Figure 1-2).

Many early papers on fossil amphibians and reptiles consisted of a description of a newly discovered herpetofauna and a paleoenvironmental interpretation based on the faunal composition, as numerous fossil amphibians and reptiles have modern analogs that are restricted in their environmental preferences, presumably due to limited environmental tolerances (e.g. Holman 1966, 1970, 1973, 1977a, 1978). For instance, Dundee and Rossman (1989) cited modern *Diadophis punctatus* (ring-necked snakes) as being restricted to forested regions with abundant rotting logs. Most natricine water snakes are found associated with permanent or semi-permanent water sources. As an example, Conant and Collins (1998) stated that *Nerodia fasciata confluens* (broad-banded watersnake) is "a snake of the great watery wilderness of the Mississippi R. delta region, and of marshes, swamps, and shallow bodies of water in general throughout its range". Furthermore, most ranid frogs, such as *Rana catesbeiana* (the bullfrog) and *Rana grylio* (the pig frog) are associated with permanent freshwater sources, whereas bufonid toads live in drier upland areas, and hylid treefrogs are mostly found living near permanent or ephemeral freshwater (Dundee and Rossman, 1989; Conant and Collins, 1998). To distinguish lowland from upland sites at Fort Polk, I constructed natricine-colubrine indices,

plotted fossil frog data on ternary diagrams, and calculated the yield of identifiable herpetofaunal elements per kilogram of matrix sieved for all Fort Polk sites.

Although there are many well-studied fossil herpetofaunas in North America, emigrations, immigrations, endemism, and originations of fossil amphibians and reptiles are not synthesized for many taxa. Furthermore, centers of diversification have not been discussed in reference to the many fossil snake, salamander, and frog taxa that suddenly appear during the Miocene. The biogeographical history of fossil herpetofaunas during the Miocene is addressed here by plotting published fossil herpetofaunal data onto North American maps to create range maps of fossil taxa through time. Most taxa described from the Fort Polk sites are plotted on a map to record distribution through time. This is done to illustrate range expansions, contractions, and/or endemism.

Traditionally, fossil amphibians and reptiles have not been used to answer stratigraphic questions like their mammalian contemporaries have been, due to their slower rates of morphological change. However, Holman (1976a and 1976b) suggested using fossil snakes to subdivide the Miocene, and he characterized Early, Middle, and Late Miocene localities in the High Plains based on snake superfamily percentages. Snakes are divided into three superfamilies by Underwood (1967): the ancient, burrowing scolecophidians, henophidians (boas, pythons, and a few less well-known groups), and modern caenophidian (colubroids) snakes (colubrids, elapids, and viperids). To determine the applicability of fossil snakes in biostratigraphy, I compiled fossil snake data for 22 North American Miocene localities, including Fort Polk. Individual species' stratigraphic ranges were plotted to produce a composite stratigraphic section for North American snakes. The ranges were plotted using the North American Land Mammal Ages of Tedford *et al*., (2004) (Figure 1-3).

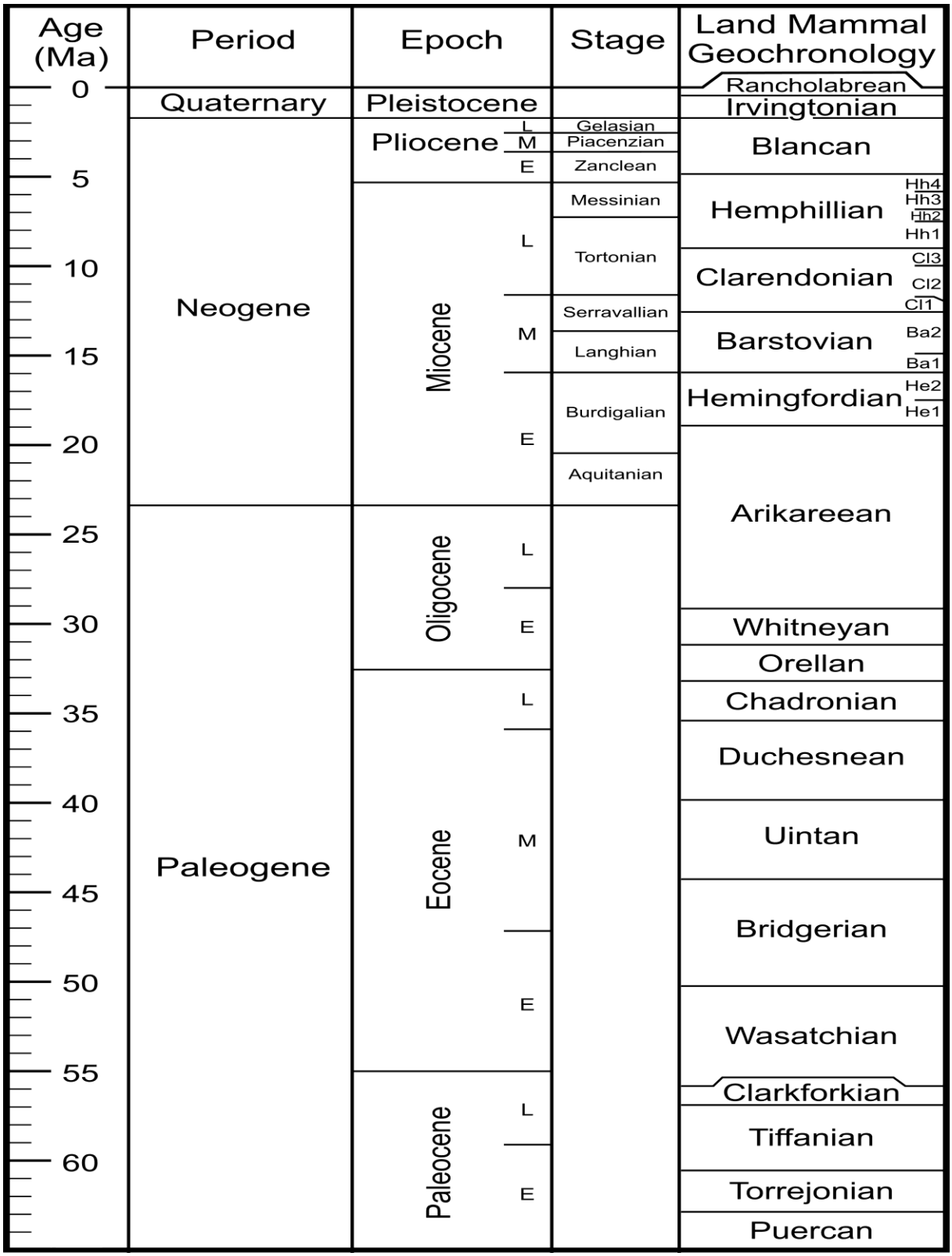

Figure 1-3. North American Land Mammal Ages, Epochs, Periods, and Ma. Modified from Holman (2006). Epochs and Stages from Lourens *et al*. (2004). Land Mammal Geochronology from Tedford *et al*. (2004).

Previous Work on Neogene Central Gulf Coast Herpetofaunas

The first reports of Miocene Gulf Coast herpetofaunas were from the Fleming Formation of eastern Texas (Figures 1-1 and 1-4; Table 1-1; Holman, 1966, 1977, 1996).

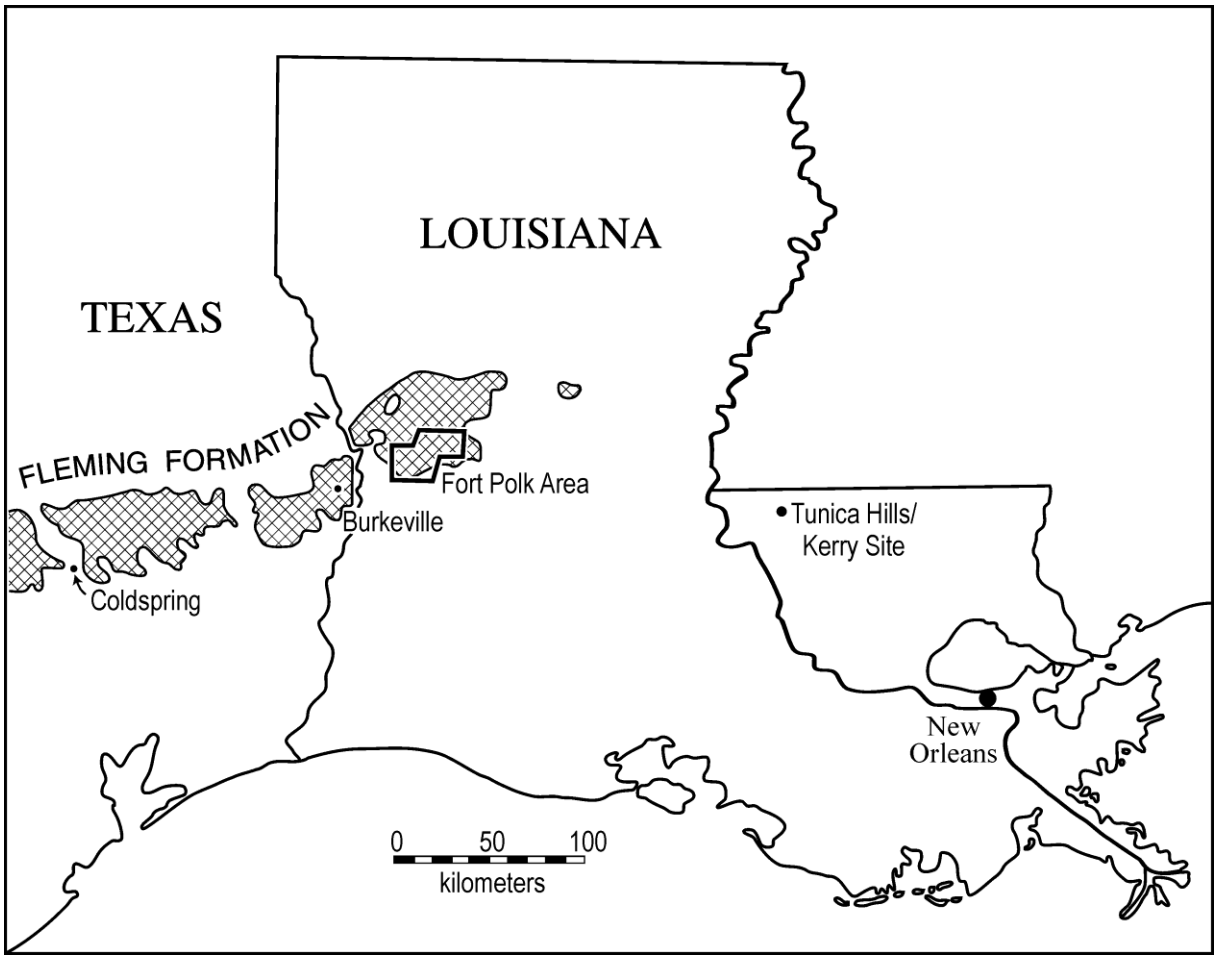

Figure 1-4. Map of Fleming Formation outcrops in east Texas and Louisiana showing The Fort Polk area and the Tunica Hills/Kerry locality. Modified from Schiebout 2001 and 2002**.**

The herpetofaunas come from four geographically and stratigraphically closely related sites: the Trinity River site in western San Jacinto County, Texas; the Moscow site in Northern Polk County, Texas; the Town Bluff site in eastern central Tyler County, Texas; and the Livingston Dam site in southern Polk County, Texas (Holman, 1966, 1977, 1996). The Trinity River site has yielded the largest numbers of specimens, including the salamanders *Notophthalmus slaughteri, Siren miotexana*, *sirenid* genus and species indeterminate, and *Amphiuma antica* (Holman, 1966,

1977, 1996). Anurans at the Trinity River site are represented by *Hyla miocenica*, *Pseudacris* cf. *P. ocularis,* and *Rana pipiens*; reptiles include an indeterminate alligator species and *Hesperotestudo* tortoise; the skink, *Eumeces miobsoletus*; and the snakes *Ogmophis miocompactus*, *Boavus affinis*, *Neonatrix infera, N. elongata, Dakotaophis greeni, Salvadora paleolineata, Texasophis fossilis,* and an indeterminate viper genus and species (Holman, 1966, 1977, 1996). The Moscow site has produced the salamanders *Batrachosauroides dissimulans, Siren miotexana, Amphiuma antica*, the boid *Calamagras weigeli*, the colubrid *Elaphe nebraskensis,* and the natricine *Neonatrix elongata* (Holman, 1977). Amphibian specimens from the Town Bluff site include the salamander *Siren miotexana* and anurans *Rana* species indeterminate and *Rana* near *Rana pipiens*, while reptiles are represented by four snake species: *Salvadora paleolineata, Elaphe nebraskensis, Texasophis fossilis,* and *Neonatrix elongata* (Holman, 1977). Finally, the Livington Dam site herpetofauna consists of a single boine trunk vertebra (Holman, 1977).

The oldest Neogene central Gulf Coast herpetofauna is the Early Miocene Toledo Bend locality (Arikareean NALMA) on the Texas-Louisiana border (Albright, 1991, 1994; Figure 1). This locality also occurs in the Fleming Formation, but is lower in the section than the previously-discussed Barstovian localities of eastern Texas. Beginning in 1989, sediments from this locality were sieved and picked for microvertebrates (Albright, 1991, 1994). The lower vertebrate fauna were described by Albright (1991 and 1994) and no subsequent material has been found, as little sieving has been done since. Albright (1991, 1994) reported from the Toledo Bend locality the salamanders *Batrachosauroides* and an amphiumid; trionychid (genus and species indeterminate), emydid (genus and species indeterminate), testudinid (*Geochelone* sp.), and dermatemydid (*Dermatemys* sp.) turtles; an indeterminate species of the lizard, *Peltosaurus*;

Alligator olseni and *Gavialosuchus* sp.; and an erycine boid, genus and species indeterminate and *Anilioides* cf. *Anilioides nebraskensis*.

Table 1-1. Comparison of numbers of reptile and amphibian taxa from east Texas Miocene sites.

Locality	Age	# of lizard genera	# of snake genera	# of crocodilian genera	# of frog genera	# of salamander genera
Trinity River, San Jacinto County, Texas	Middle Miocene	1	8	1	2	3
Moscow Site, Moscow County, Texas	Middle Miocene	0	3	0	0	3
Town Bluff Site, Tyler County, Texas	Middle Miocene	0	4	0	2	1
Livingstone Dam Site, Polk County, Texas	Middle Miocene	0	1	0	0	0
Toledo Bend Site, Newton County, Texas	Early Miocene	1	2	2	0	2

The only previously reported central Gulf Coast Miocene herpetofauna east of the Mississippi River was the early Barstovian Willacoochee Creek Fauna from the eastern Florida panhandle (Bryant 1991). The herpetofauna is small in terms of the number of specimens, but is fairly diverse, considering the low specimen counts. The herpetofauna includes the salamander *Batrachosauroides dissimulans*; two colubrine and one natricine snake; and lizards represented by the families Iguanidae (? *Leiocephalus*), Teiidae (? *Cnemidophorus*), Scincidae, and Helodermatidae (Bryant, 1991).

Among the central Gulf Coast Miocene herpetofaunas described in this study, the deposits from the Middle Miocene (Barstovian NALMA) Fort Polk locality coincided with the regressive

phase of the *Potamides matsoni* zone and were dated using mammalian biostratigraphy and magnetostratigraphy (Figures 1-4, 1-5; Schiebout, 1997; Schiebout and Ting, 2001; Schiebout *et al*., 2002; Schiebout *et al*., 2004 and Williams and Schiebout, 2003).

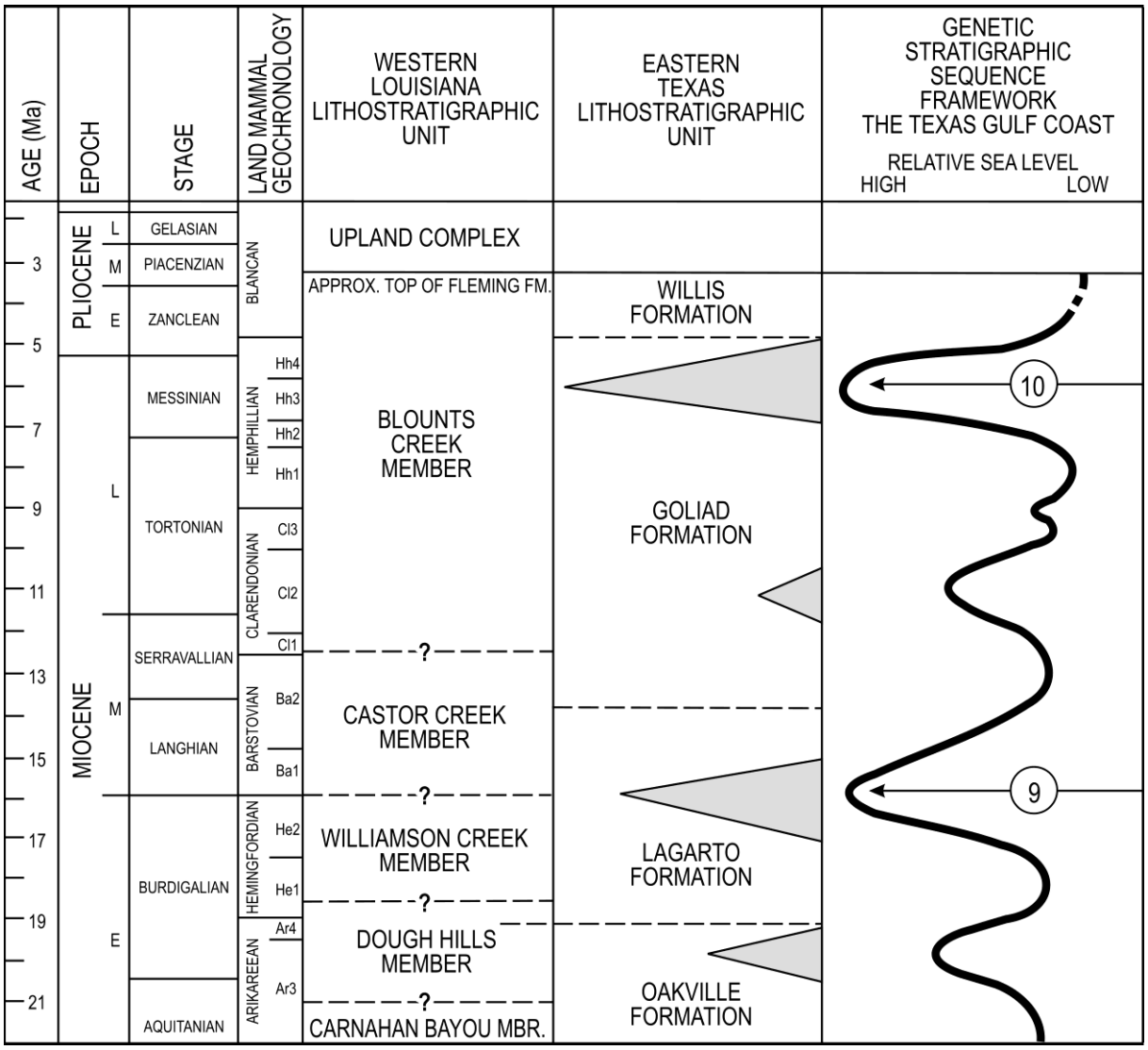

Figure 1-5. Summary correlative events chart including Age (Ma), Epochs, and Stages from Lourens *et al*. (2004). Land mammal geochronology of Woodburne and Swisher (1995), western Louisiana lithostratigraphic units from Hinds (1999), relative sea level with numbers representing genetic sequence stratigraphic boundaries (Galloway et al., 1991; Hinds, 1999). Figure modified from Schiebout and Ting (2001).

Previous to this study, no comprehensive identifications and descriptions of the Fort Polk herpetofauna were published, although some preliminary work was performed (Schiebout 1997;

Schiebout and Ting 2001; Schiebout *et al.*, 2002, 2004; Williams and Schiebout 2003; Williams 2005). The presence of crocodilians from Fort Polk has also been reported (Schiebout 1997; Schiebout and Ting 2001; Schiebout *et al.*, 2002; Schiebout *et al*, 2004). The material consists of isolated teeth and partial vertebral centrum and has been identified as *Alligator* sp. and *Gavialosuchus* sp. (Schiebout, 1997). Turtles from the Fort Polk sites include shell fragments from an indeterminate species and genus of tryonichid and two well-preserved tortoise shells, both with articulated carapaces and plastrons that are assigned to the genus *Hesperotestudo* (Schiebout 1997; Williams in Schiebout *et al*., 2004). Previously-described squamates from the Fort Polk locality include a lizard dentary (Schiebout, 1997), a squamate dentary (Schiebout *et al*., 2004), natricine and colubrine snakes (Schiebout and Ting, 2001; Schiebout *et al*., 2004), and an indeterminate viperid (Schiebout *et al*., 2004). Finally, anurans have been reported from Fort Polk and are represented by a single sacrum from a bufonid toad (Schiebout and Ting, 2001).

Currently, the Late Miocene (Hemphillian NALMA) Tunica Hills/Kerry locality is yielding a herpetofauna, briefly discussed in Schiebout *et al*. (2006), which then consisted only of tryonichid shell fragments, unidentified chelonian shell fragments, and a single crocodilian tooth from 38.6 kg of wet-screened clays.

Methods

The fossil amphibians and reptiles reported in this study were collected and processed in several ways. With the exception of the larger turtles and crocodilians, which were generally collected on the surface, most of the herpetological material was recovered using wet screening methods (Schiebout *et al*., 1998). Bulk consolidated and unconsolidated sediment samples were transported from the field to the laboratory in large, woven plastic bags, which had been labeled

with a permanent marker. Once in the laboratory, rock or unconsolidated sediment samples were weighed and placed into ten gallon plastic containers to soak in water for the unconsolidated clays and 10% glacial acetic acid for indurated rocks. The acetic acid was used to dissolve the calcium carbonate cement and nodules found in Fort Polk sites in indurated rocks, whereas the Tunica Hills/Kerry locality and other Fort Polk sites, such as TVOR Southeast, only required a soak in water, because the clays which contained the specimens, are unconsolidated. Disaggregated materials were then wet-screened under running water using a coarse screen (1-3 mm) mounted on top of a fine screen with 0.59 mm mesh. The residue left behind consisted of siliceous minerals, clay minerals, bones, and teeth and was placed on large metal trays for drying. When dry, the washed matrix was picked under binocular microscopes, separating the bones and teeth from the other residue.

Geographic, Geologic, and Stratigraphic Settings

During the Cenozoic, Louisiana prograded seaward as sediments from the Rocky Mountains and Appalachian Mountains were deposited in the form of clastic wedges that thickened from north to south (Hinds, 1999). Thus, surface exposures are older in the northern part of the state and younger in the south. Many Cenozoic deposits have a slight dip to the south and outcrop in distinct northeast to southeast bands across Louisiana and Texas (Figure 1-4).

The Toledo Bend and Fort Polk localities are part of the Fleming Formation, which outcrops in a discontinuous, northeast to southeast trending strip (Figure 1-4). Fisk (1940) divided the Fleming Formation into six members, a division which is still in use today. The Toledo Bend locality lies within the Carnahan Bayou Member of the lower Fleming Formation, which is

above the Lena and below the Dough Hills Members (Figure 1-5 and 1-6; Albright, 1991, 1994, 1996).

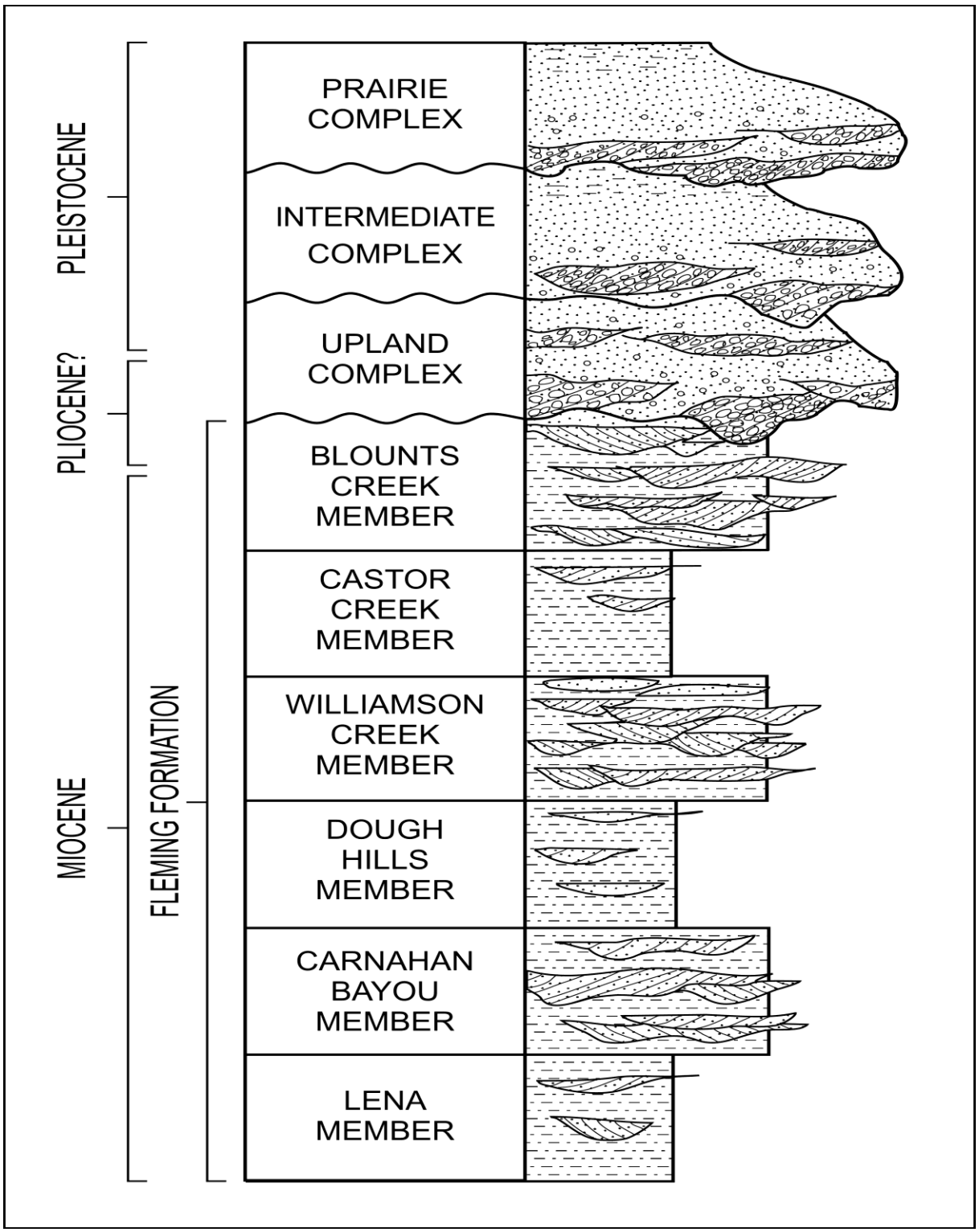

Figure 1-6. Fleming Formation members. From Hinds (1999).

The outcrop consists of fossiliferous conglomerates, which are exposed over an approximately 40 m^2 area, and are up to two meters thick (Albright, 1991, 1994, 1996). Sediments from the Toledo Bend local fauna were deposited at ~23 Ma during the Arikareean NALMA (Albright, 1991, 1994, 1996, 1998a, 1998b). This early Miocene age was determined using mammalian biostratigraphy and is mostly based on ungulate mammals (which were all browsers). The fauna has strong affinities to the well-documented middle Arikareean from Florida and the Great Plains (Albright, 1991, 1994, 1996).

The geological setting of the various herpetofaunal-bearing sites at Fort Polk affords an opportunity to study paleoenvironments using fossil amphibians and reptiles from sites that are in extremely close geographical proximity (~ 4 km^2), and are close in age (from 13.8 to 13.1 Ma based on paleomagnetic data and mammalian biostratigraphy), but represented a range of environments from transitional marine to terrestrial lowland and upland, possibly similar to Pleistocene terraces found in modern Louisiana (Figures 1-7 and 1-8; Schiebout, 1997; Schiebout and Ting, 2001; Schiebout *et al*., 2002; Schiebout *et al*., 2004). There are eight fossiliferous sites within Fort Polk, and six of them have produced fossil amphibians and/or reptiles. All Fort Polk sites are part of the Castor Creek Member of the Fleming Formation. The Castor Creek Member is near the top of the Fleming Formation, and is underlain by the Williamson Creek Member and overlain by the Blounts Creek Member (Figure 1-5 and 1-6; Hinds, 1999; Schiebout, 1997; Schiebout and Ting, 2001; Schiebout *et al.,* 2002; Schiebout *et al.,* 2004). Although thickness estimates vary, the most recent estimate is between 137 and 152 meters (Hinds, 1999).

As was previously mentioned, the late Barstovian NALMA (Ba2 of Tedford *et al*. (2004)) of the Fort Polk sites is tightly constrained and well-supported by mammalian biostratigraphy and

paleomagnetic dating (Figure 1-8 and 1-9; Schiebout, 1997).

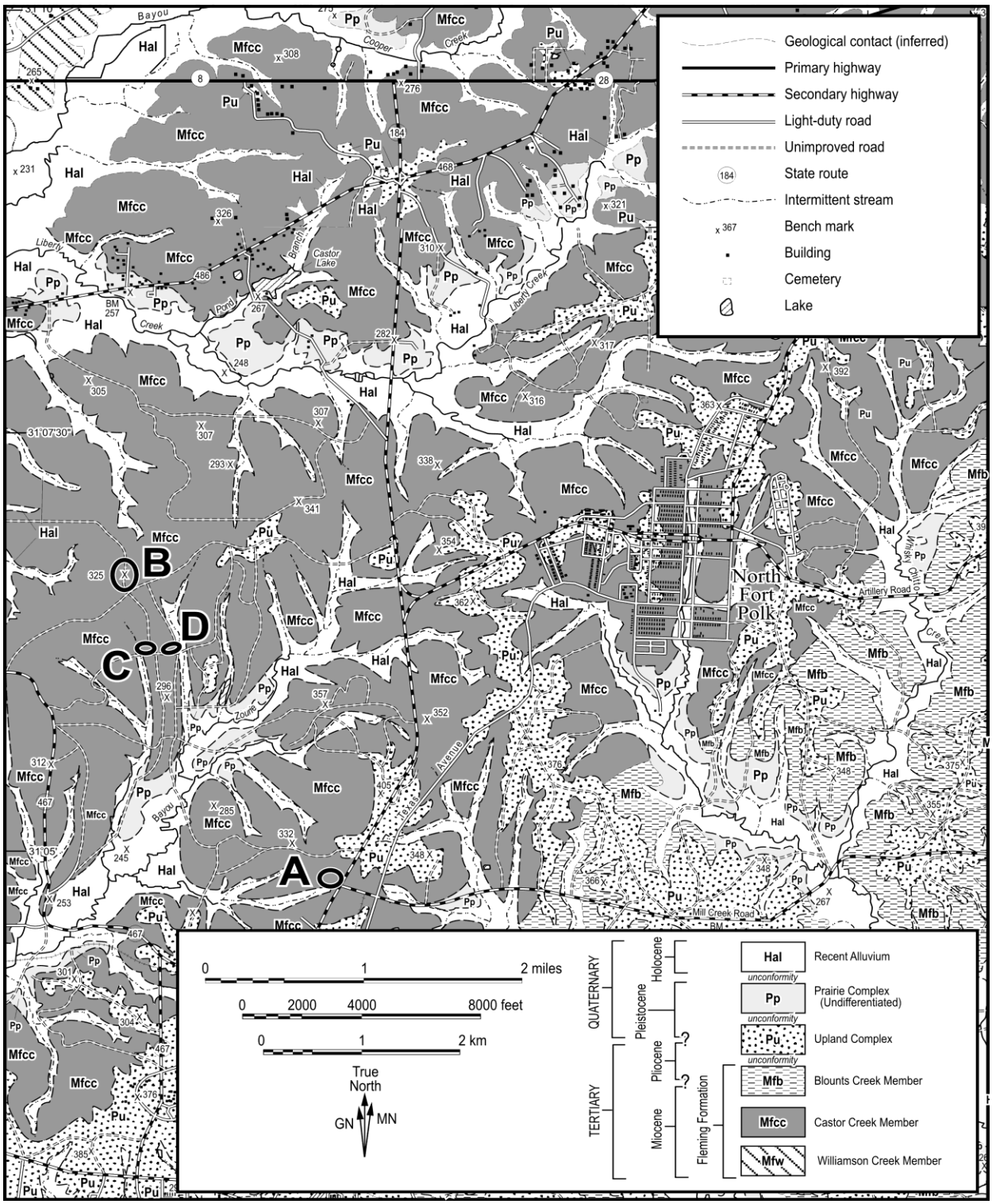

Figure 1-7. Fort Polk vertebrate-bearing sites. A. Discovery Site (DISC) cluster; B. TVOR (Terminal Very High Frequency Omni Radar) Site; C. TVOR South; D. TVOR SE. Modified from Schiebout et al. (2004). Geologic map from Hinds (1999).

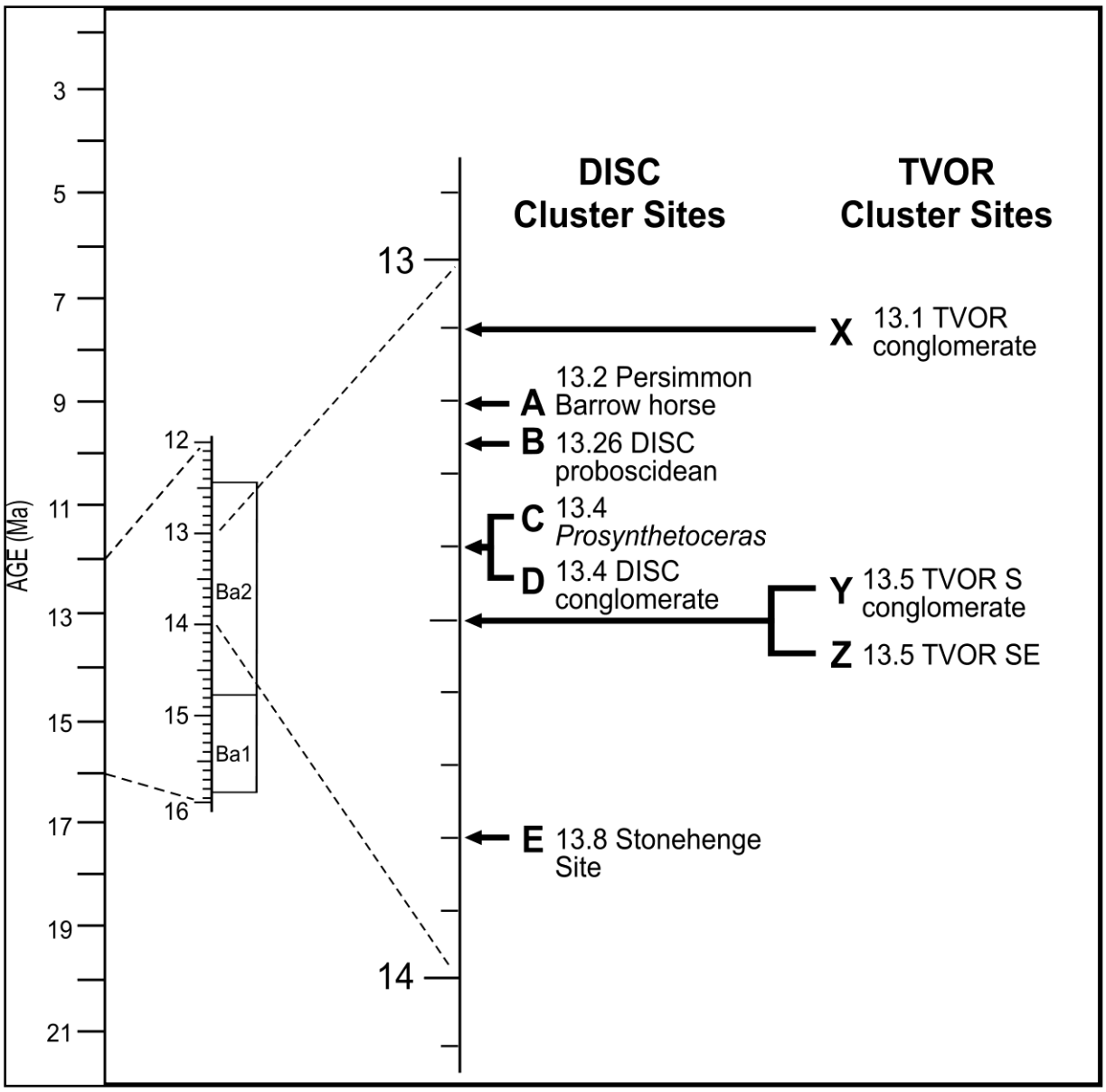

Figure 1-8. Paleomagnetically derived ages of Fort Polk sites in Ma. From Gose *et al*. (2008).

The presence of the proboscidean, *Gomphotherium* sp., the prosynthetocerine camel, *Prosynthetocerous francisi,* and the horse, *Cormohipparion,* place the Fort Polk locality within late Barstovian NALMA, specifically within the Cold Spring local fauna of Wilson (1956), which overlie the Burkeville local fauna (Figure 1-9; Schiebout, 1997; Schiebout *et al*, 2002). Recent paleomagnetic data from Gose *et al* (2008) indicate that the Stonehenge site is the oldest

at 13.8 Ma and the 13.1 Ma TVOR conglomerate is the youngest (Figure 1-7).

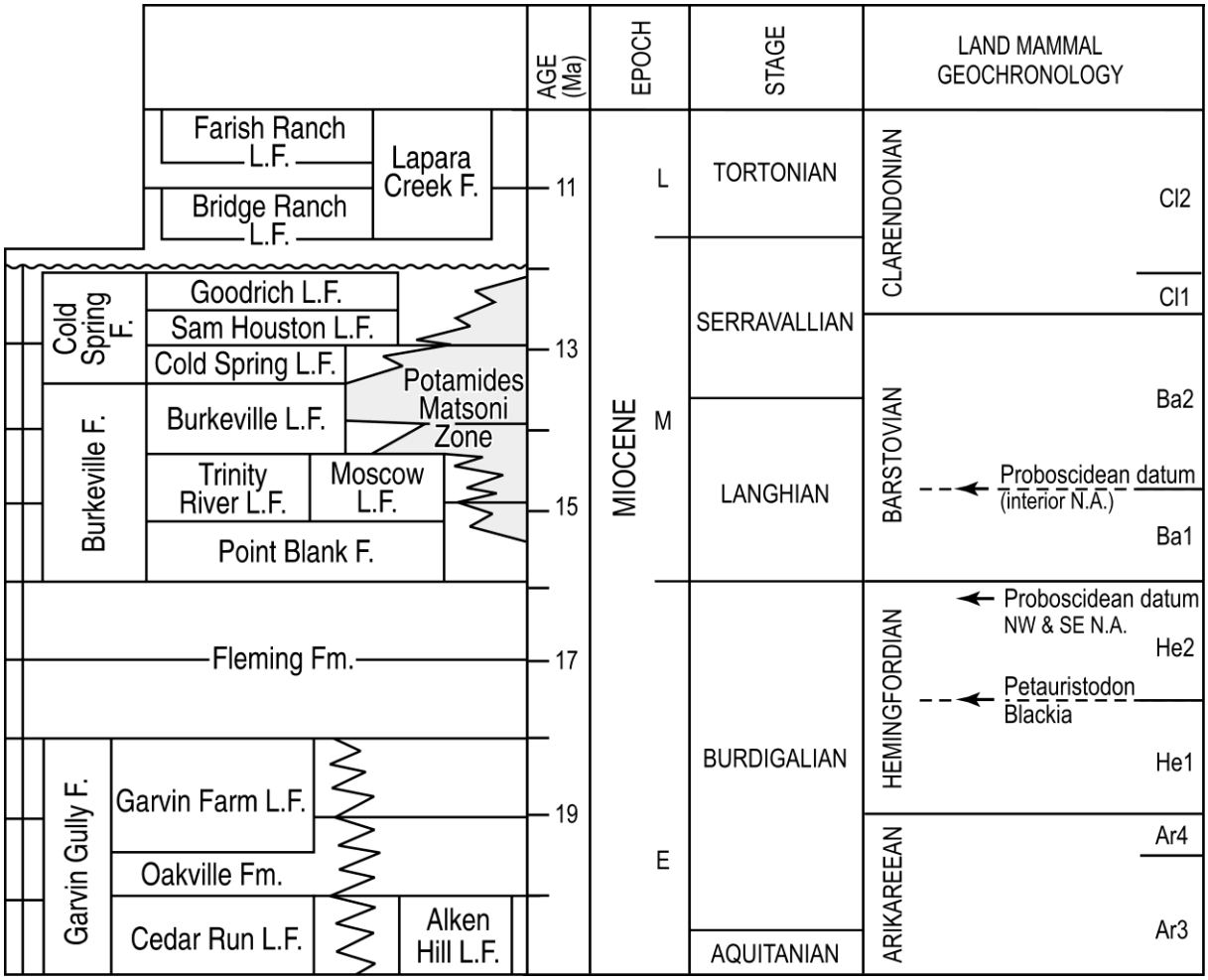

Figure 1-9. Fleming Formation vertebrate faunas in east Texas, age (Ma), Epochs, and Stages from Lourens (2004). North American Land Mammal Ages with biostratigraphic markers from Tedford *et al*. (2004).(Modified from Tedford *et al*., 1987, 2004).

Much of the Castor Creek Member is composed of clay deposits. However it does contain some lenses composed of very fine to coarse sands and conglomerates (Figure 1-6). The conglomerates and sands are rich in calcium carbonate pedogenic nodules and produce fossil microvertebrates (Schiebout, 1997; Schiebout *et al*., 1998). The main fossil-bearing deposits within the Discovery site, a barrow pit next to a landfill, are composed of conglomerate layers (Schiebout, 1997; Schiebout *et al*., 1998). Trough cross beds are seen in some exposures, and Schiebout (1997) considered the depositional environment to be an irregular series of reworked

soil layers deposited as lag deposits, some in small channels. The Stonehenge site, situated less than one kilometer south of the DISC site, is exposed in a narrow creek. Isolated chunks of conglomerate were recovered using heavy equipment (Schiebout, 1997). The TVOR site also contains scattered conglomerate lenses (Schiebout, 1997). Two other sites, TVOR Southeast and South (Figure 1-7), are currently under study by Julie Hill. TVOR Southeast was determined to represent a shallow marine environment in which an *in situ* oyster bed was found overlain by clay-containing terrestrial and deep marine fossils that ranged in size from large camel limb bones to microfossils, such as insectivores and rodents (Schiebout *et al*., 2002, 2004). Based on the lack of sorting of marine and terrestrial organisms in a section that is less than a meter in thickness, Schiebout *et al.* (2002, 2004) considered the site to be a storm deposit from a hurricane coming from the Gulf of Mexico. This section contains whale bones and large grouper fish spines that are deposited on or above the oyster bed, all found with terrestrial vertebrate bones that were transported into the near-shore environment by a river.

The TunicaHills/Kerry locality is located in East Feliciana Parish in south central Louisiana (Figure 1-1). It is part of the Pascagoula Formation, and was tentatively considered to be Late Miocene (Hemphillian NALMA), between Hh-2 and Hh-4 of Woodburne (2004) (approximately 8.5-4.5 Ma), based on the artiodactyls and perrisodactyls recovered thus far (Schiebout *et al*., 2006). The presence of the rhinoceros *Teleoceras*, horses similar to *Neohipparion eurystyle, Nannippus, Cormohipparion*, the antilocaprid, *Hexameryx*, and a lamine genus, *Pleiolama* or *Alforjas*, all support this age determination (Schiebout *et al*., 2006).

Self (1989) reported both fluvial and shallow marine paleoenvironments from the Pascagoula Formation. Schiebout *et al*. (2006) considered it to be an estuarine paleoenvironment because the sediments display an extreme degree of bioturbation and sedimentary structures indicative of

estuarine environments. Lithologically, TunicaHills/Kerry is composed of unconsolidated clays.

CHAPTER 2: FORT POLK AND TUNICAHILLS/KERRY SYSTEMATIC PALEONTOLOGY

Introduction

Understanding the taxonomy and biogeographical history of fossil animals is important, as it has implications for ancient climatic changes and regional and local tectonics.

The purpose of this chapter is twofold. First, I compared the herpetofaunal elements from Fort Polk and TunicaHills/Kerry localities with Miocene herpetofaunas from Florida, east Texas, and Nebraska, and with modern osteological specimens, to determine the taxonomic affinities of the herpetofaunas. After description of the Fort Polk herpetofauna, I mapped the geographic ranges of the Fort Polk taxa through time to determine if immigrations, centers of distribution, or endemism can be recognized.

Methods

Some taxa are mapped at the generic level if meaningful biogeographic inferences are obtainable, such as temporal and/or geographic range extensions or endemism. The maps are subdivided by North American Land Mammal Ages and were originally produced using Google Earth to plot occurrences by county, and then were transferred to a North American map. For instance, all Miocene sites that are Barstovian land mammal age and have a particular taxon received a dot representing the presence of that taxon in that county during the Barstovian. Where locality ages have been designated early, middle, or late for the given land mammal age, symbols are used to separate the different ages.

Class Amphibia Linnaeus, 1758

Order Caudata Oppel, 1811

Family Sirenidae Gray, 1825

The Neogene fossil record of salamanders is fairly extensive, with most taxa being described on the basis of trunk vertebral characteristics (Holman, 1995, 2006). Some important diagnostic characteristics include the centrum condition (procoelus or amphicoelous), neural arch and spine morphology, neural canal shape, pre- and postzygapophyseal articular facets, and the bicapitate rib bearers (Figure 2-1). Unfortunately, the salamander appendicular skeleton is largely cartilaginous and easily destroyed during transport and the fossilization process. Therefore it is not commonly found at fossil sites (Holman, 1995, 2006; Boardman, 2009).

Genus *Siren* Linnaeus, 1766

Siren miotexana Holman, 1977a

Figures 2-2, 2-3, and 2-4

Referred material. ─ LSUMG V-9764, 20902, 20903, 20904, 20905, 20906, 20907, 20908, 20909, 20910, 20911, 20912, 20913, 20914, 21164, 15 trunk vertebrae from the Stonehenge site; LSUMG V-20979, 20980, two trunk vertebrae from the TVOR site; LSUMG V-20915, 20916, two vertebrae from the TVOR SE site.

Description. ─ These small vertebrae are opisthocoelus with a notochordal canal extending through the centra and when preserved, aliform processes on the dorsal surface of the neural arch that diverge at approximately 70°. Ventrally, they all have prominent, thin ventral keels that are flanked by large subcentral foramina; however, there is considerable variation in the amount of ventral keel development between individual vertebrae from Fort Polk and east Texas. The gently curving zygapophyseal ridges meet the transverse processes near the base of the prezygapophyses.

Discussion. ─ Members of the family Sirenidae are the most basal salamander family and

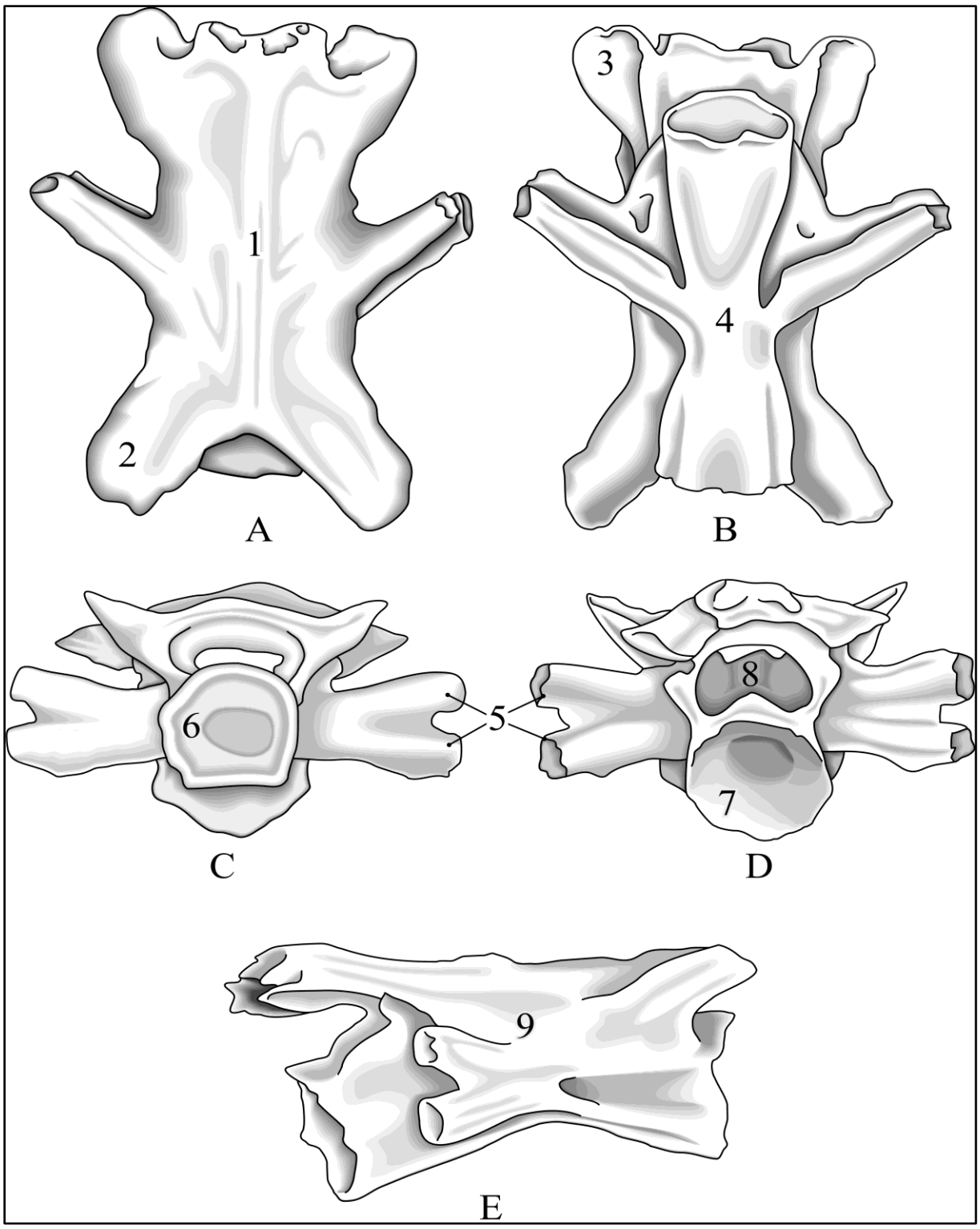

Figure 2-1. Generalized *Ambystoma* salamander vertebra in (A) dorsal, (B) ventral, (C) anterior, (D) posterior, and (E) lateral views. 1, neural spine; 2, prezygapophyseal articular facet; 3, postzygapophyseal articular facet; 4, centrum (ventral view); 5, bicapitate rib bearers; 6, anterior cotyle; 7, posterior cotyle; 8, neural canal; 9, lateral wall of neural arch. Modified from Holman (2006).

have a fossil record in North America that extends back to the Late Cretaceous of Alberta and Saskatchewan, Canada (Holman, 2006). Goin and Auffenberg (1957) named *Siren dunni* from the Wyoming Eocene on the basis of isolated vertebrae, and this remains the oldest record of the genus in North America. *Siren* does not appear again in the fossil record until the Hemingfordian with the appearance of *Siren hesterna* from the Thomas Farm locality in central Florida (Figure 2-3; Goin and Auffenberg, 1955; Holman, 2006). The Fleming Formation in east Texas and western Louisiana, along with the Valentine Formation in northern Nebraska, have produced Barstovian representatives of the genus (Figure 2-4; Holman, 1966, 1977a, 1996, 2006; Holman and Voorhies, 1985). There are no Clarendonian *Siren* specimens known, but *Siren simpsoni* has been described from Hemphillian deposits in Alachua County, Florida (Figure 2-5; Goin and Auffenberg, 1955; Holman, 2006).

Modern members of the family include *Siren* (two species) and *Pseudobranchus* (one species) and are found in the eastern United States and northern Mexico (Goin and Auffenberg, 1955; Holman, 2006). They are obligatorily aquatic, have eel-like bodies, and lack hind limbs (Goin and Auffenberg, 1955; Holman, 2006). *Siren miotexana* is only known from the early Barstovian east Texas Miocene sites within the Fleming Formation (Holman, 1966, 1977a, 1996, 2006).

The assignment of the referred specimens to *Siren miotexana* is based on the 70° angle formed between the aliform processes (Figure 2-2). The angle between the aliform processes in the Hemingfordian taxon, *S. hesterna*, from the Thomas Farm locality, is approximately 123° (Goin and Auffenberg, 1955; Holman, 2006). The other known Miocene Gulf Coast taxon, *S. simpsoni*, from the Hemphillian Haile Pit VI locality in Florida, has a zygapophyseal ridge that has little to no downward curvature when viewed laterally. The Fort Polk *Siren* vertebrae are excluded from *Pseudobranchus*, which are similar to *Siren*, based on characters originally

outlined by Goin and Auffenberg (1955) and reiterated by Holman (2006). When viewed laterally, the ventral border of the centrum in *Siren* is less concave than *Pseudobranchus.* The zygapophyseal ridge of *Siren* is generally straight or slightly curved and connects to the transverse process at the bottom of the prezygapophyses; whereas, the zygapophyseal ridge of *Pseudobranchus* has a downward curve and connects to the transverse process posterior to the base of the prezygapophyses.

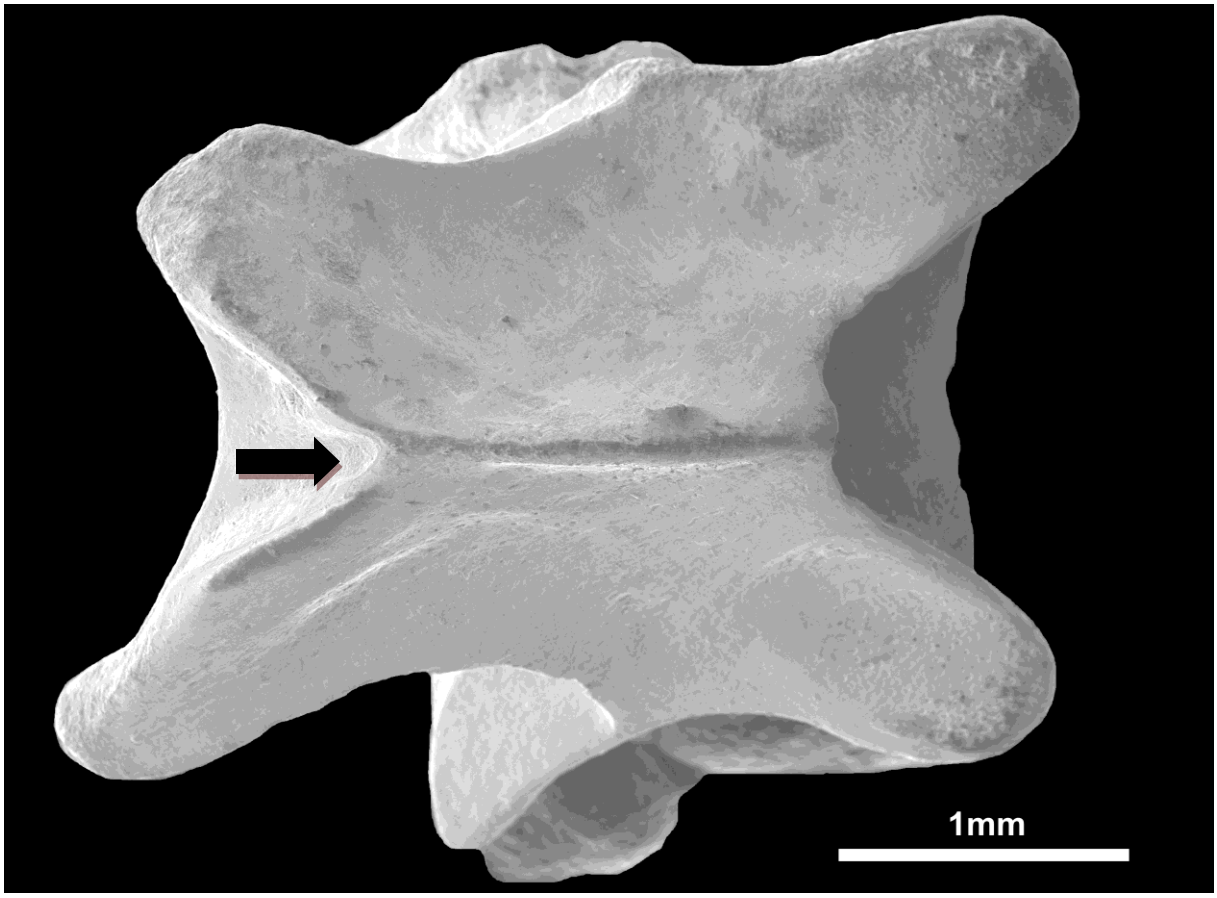

Figure 2-2. Scanning electron micrograph of *Siren miotexana* (LSUMG V-9674) in dorsal view. The black arrow points to the angle between the aliform processes.

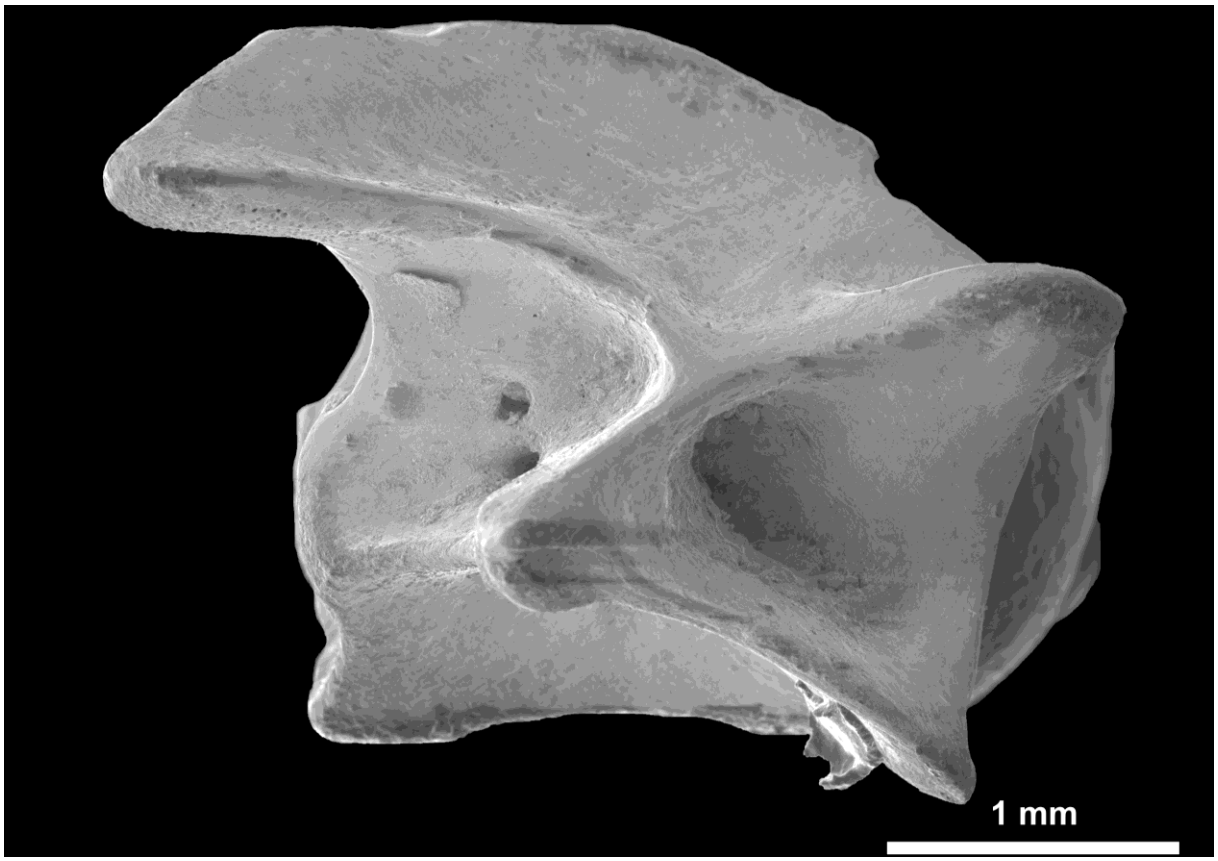

Figure 2-3. Scanning electron micrograph of *Siren miotexana* (LSUMG V-9674) in left lateral view.

Figure 2-4. North American distribution of Hemingfordian *Siren*.

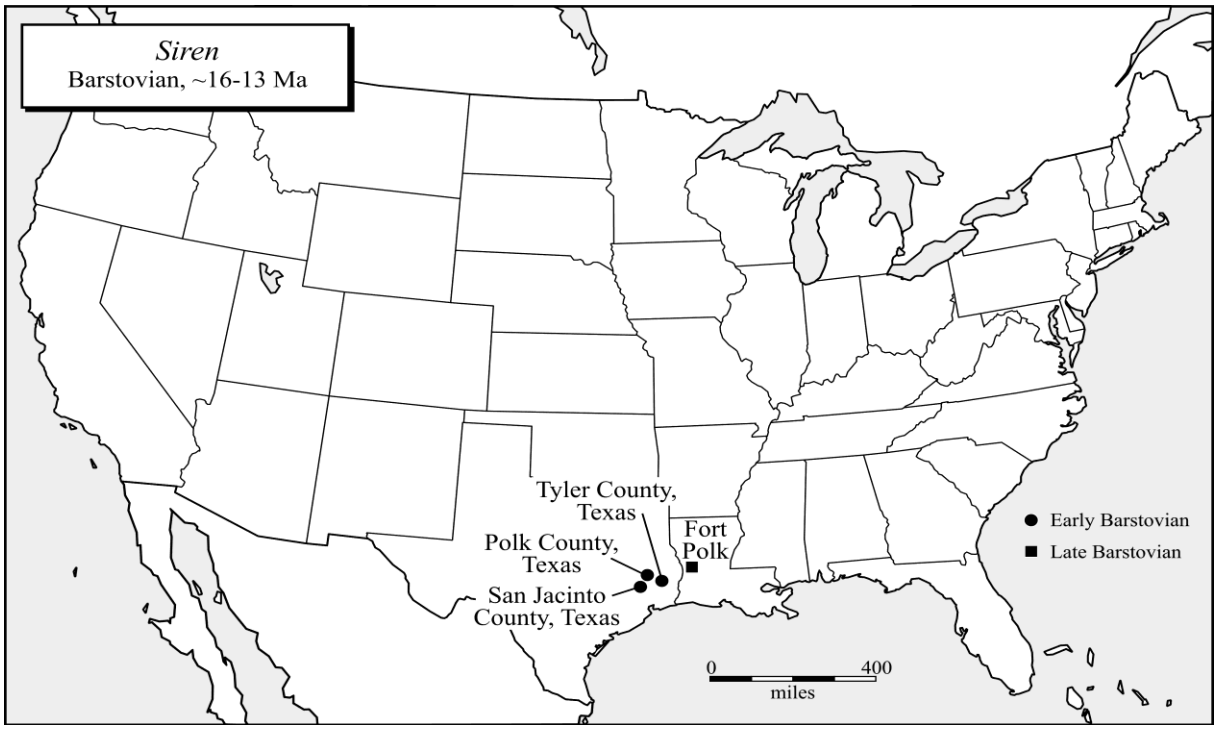

Figure 2-5. North American distribution of Barstovian *Siren.*

Siren species indeterminate

Referred material. ─ LSUMG V-20988, 20989, 20990, 20991, 20992, 20993, 20994, 20995, 20996, 20997, 21137, 21138, 21139, 21140, 21141, 21142, 21143, 21167, 21170, 19 fragmentary vertebrae from the Stonehenge site; LSUMG V-20921, one fragmentary vertebra from the TVOR SE site.

Description/Discussion. ─ These fragmentary vertebrae are considered *Siren* based on the zygapophyseal ridge and transverse process morphology outlined above, and the ventral keel flanked by prominent foramina. Unfortunately the neural arches are not preserved, so it cannot be determined whether the aliform processes diverged at a 70° angle as in *Siren miotexanus*.

Family Salamandridae Gray, 185

Genus *Notopthalmus* Rafinesque, 1820

Notopthalmus slaughteri Holman, 1966

Figures 2-6, 2-7, 2-8, and 2-9

Referred material. ─ LSUMG V-20998, 20999, 21000, 9121, four vertebrae from the Stonehenge site.

Description. ─ Viewed dorsally, these opisthocoelus vertebrae have neural spines that rise above the neural arch, although they are broken. The neural spines ascend posterodorsally where they flair into a "V" above the postzygapophyses. The prezygapophyses are rounded to subrounded. In posterior view, the neural canals are ventrally flattened, vertically elongated, and arched dorsally. The cotyla are oval with their dorsal border flat. The rims around the cotyla are damaged. The postzygapophyses have a moderate upward tilt. The rib-bearers are broken off before their terminus.

Discussion. ─ The fossil record of *Notopthalmus* begins in the Hemingfordian of South Dakota and Florida with *Notophthalmus crassus* and *Notophthalmus robustus*, respectively and continues to the present, with extant species of eastern newts, *Notophthalmus viridescens*, *N. meridionalis* and the striped newt, *N. perstriatus*, found from eastern Texas to Florida up to southern Canada (Estes, 1963; Tihen, 1974; Conant and Collins, 1998; Holman, 2006). The fossil record of *N. viridescens* only extends back to the Irvingtonian, and no *Notophthalamus* are known between the Irvingtonian and the late Barstovian specimens from Fort Polk (Holman, 2006).

Notopthalmus slaughteri is only known from the holotype specimen (SMPSMU 61870) from the early Barstovian Trinity River locality in east Texas, so the addition of three new specimens from the late Barstovian Stonehenge site is an important contribution to our understanding of the animal (Holman, 1966; 2006). In all aspects, the Fort Polk specimens compare well with the

holotype from Texas. Holman (2006) noted a trend in *Notopthalmus* from the Early to Middle Miocene, in that the Hemingfordian taxa *N. robustus* from the Thomas Farm locality in Florida and *N. crassus* from Batesland Formation of South Dakota are more robust and were deemed more primitive, as modern *Notopthalmus* vertebrae are of a much lighter build. In this respect, the Louisiana specimens are similar to the more derived taxa.

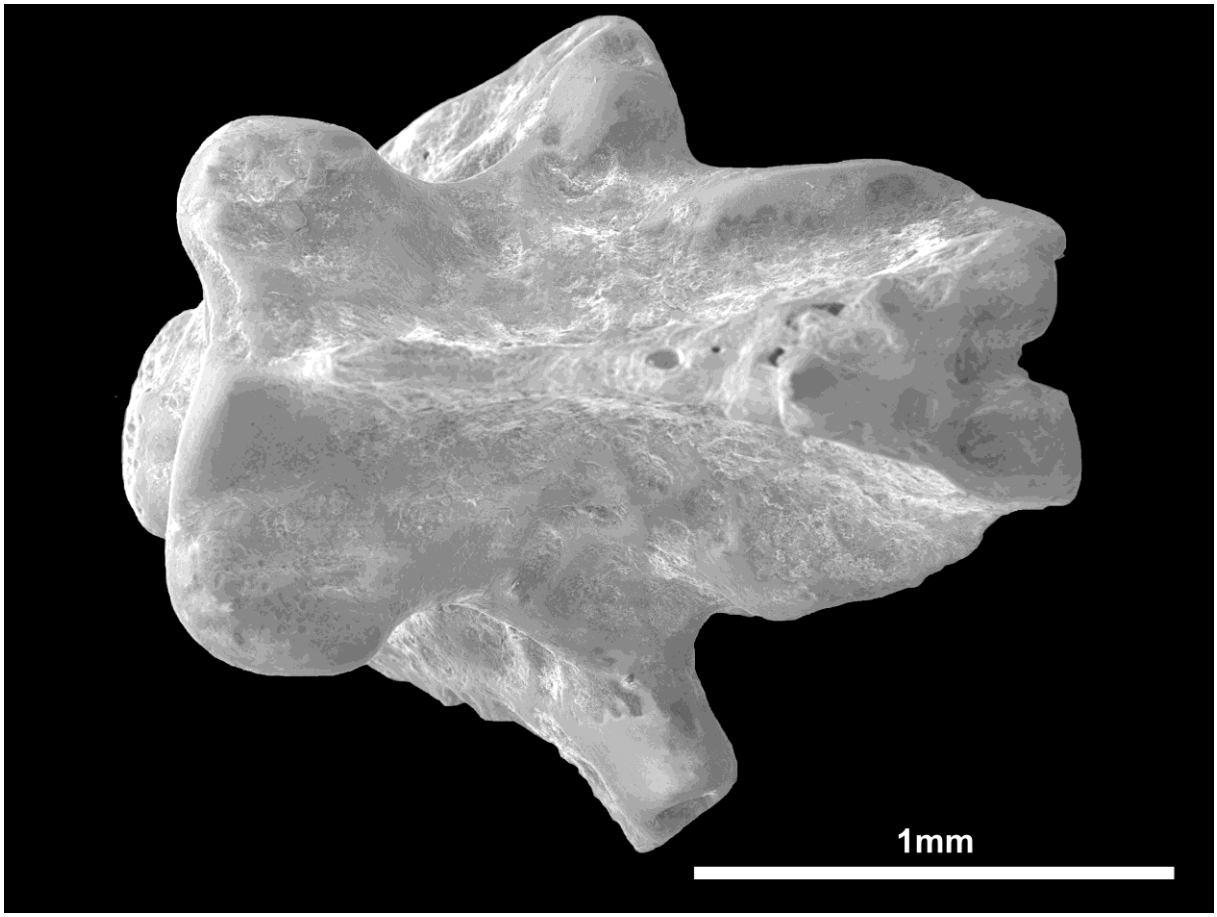

Figure 2-6. Scanning electron micrograph of *Notophthalmus slaughteri* (LSUMG V-20998) vertebra in dorsal view.

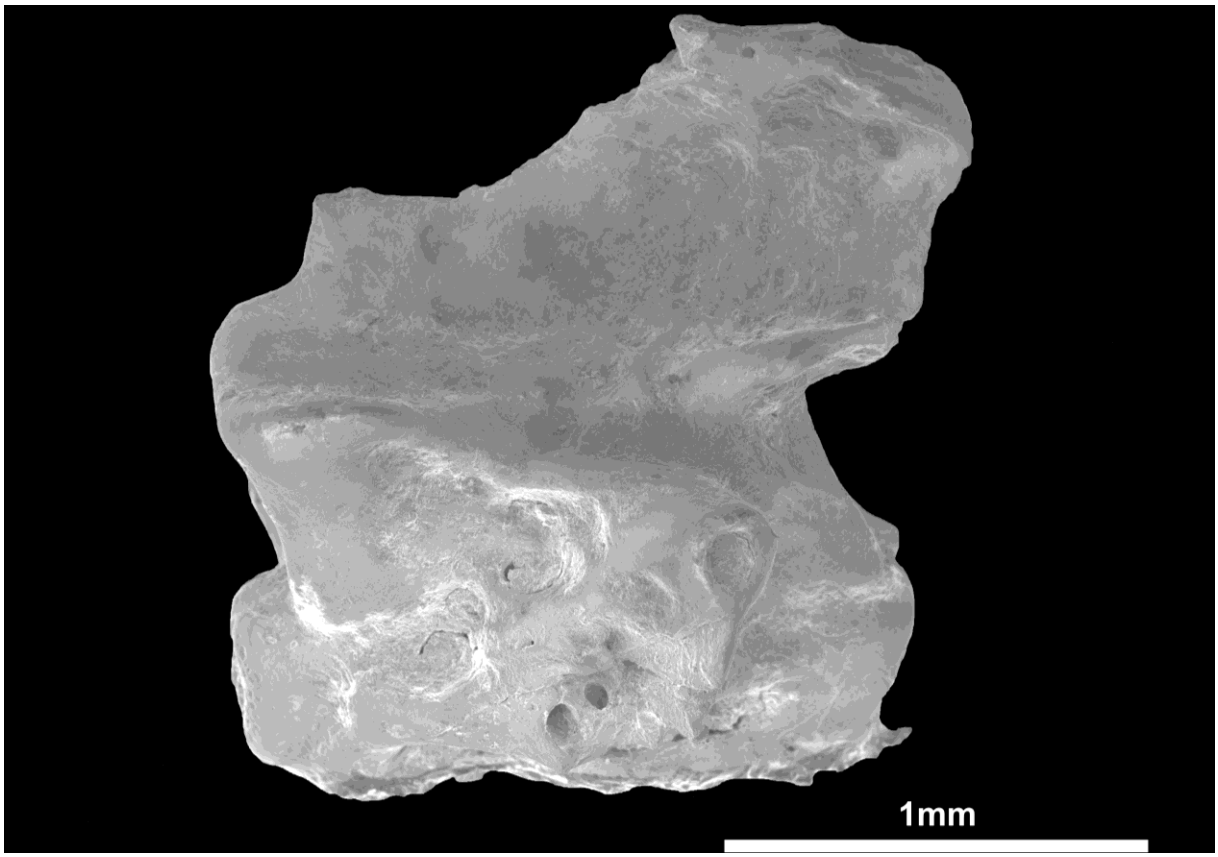

Figure 2-7. Scanning electron micrograph of *Notophthalmus slaughteri* (LSUMG V-20998) vertebra in right lateral view.

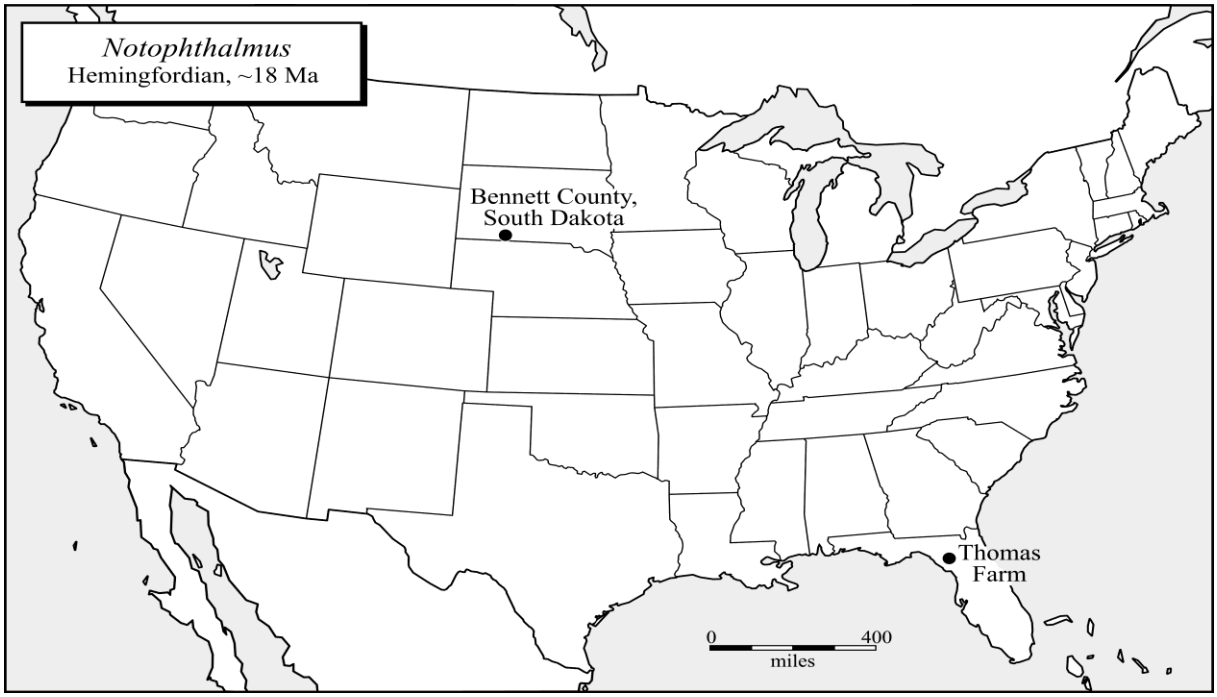

Figure 2-8. North American distribution of Hemingfordian *Notophthalmus.*

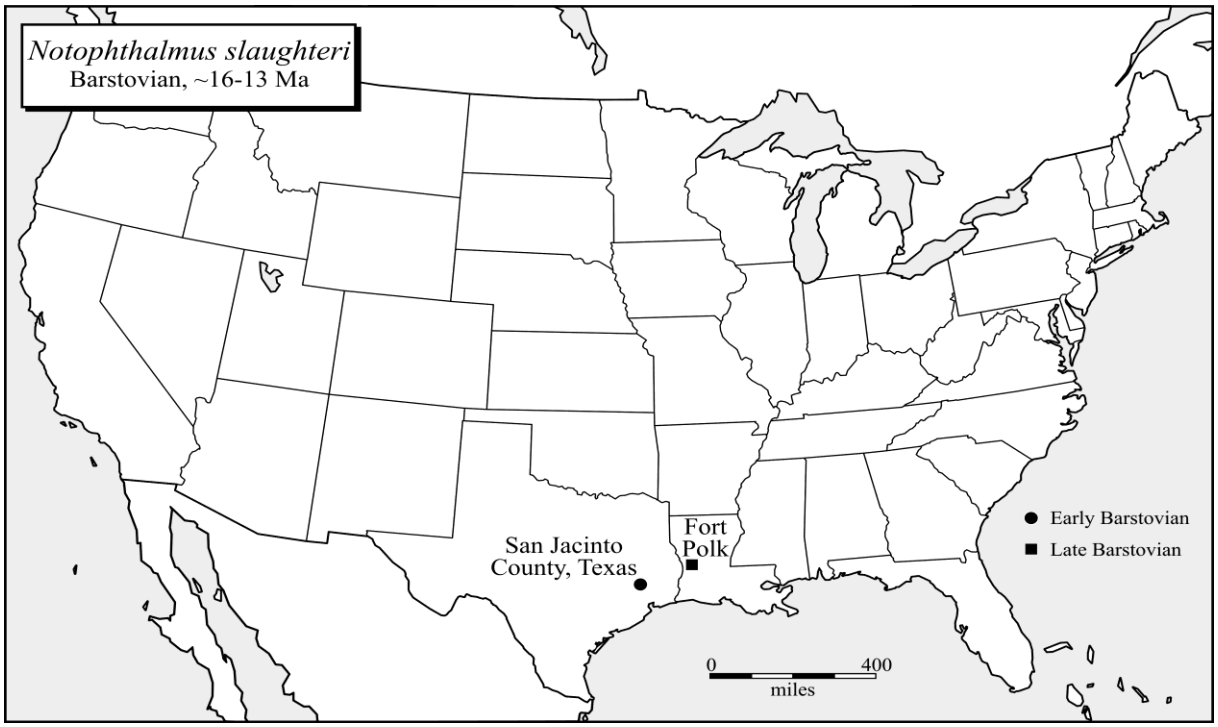

Figure 2-9. North American distribution of Barstovian *Notophthalmus.*

Family Batrachosauroididae Auffenberg, 1958

Genus *Batrachosauroides* Taylor and Hesse, 1943

Batrachosauroides cf. *Batrachosauroides dissimulans*

Figures 2-10, 2-11, 2-12

Referred material. ─ LSUMG V-13858, one vertebra from the TVOR site.

Description. ─ This vertebral centrum represents the largest salamander vertebra from the Fort Polk Miocene. The vertebra is opisthocoelus and has a notochordal canal in the middle of the cotyle. The condyle has a calcified cartilaginous ring on it, and there is a round depression in the center of the condyle that penetrates fairly deeply. There is a pronounced median keel (hypapophysial keel of Auffenberg, 1958 and Albright, 1994) that flairs anteriorly and posteriorly and is moderately constricted in the middle. No foramina are present adjacent to the median keel. The neural arch is missing. The transverse processes and rib-bearers are broken.

Discussion. ─ *Batrachosauroides* is a member of the extinct salamander family Batrachosauroididae, which has a fossil record extending back into the Early Cretaceous of Texas with *Prosiren elinorae* and culminated with the presence of *Peratosauroides problematica* from the Hemphillian of California (Holman, 2006). The earliest record of *Batrachosauroides* is from the Early Eocene (Wasatchian) of North Dakota represented by *Batrachosauroides gotoi* (Estes, 1981; Holman, 2006). No *Batrachosauroides* species are known from the Oligocene. Albright (1994) described the first known *Batrachosauroides* since the Eocene taxon *Batrachosauroides gotoi* and determined it was comparable to *Batrachosauroides dissimulans* (Figure 2-10; Albright, 1994; Holman, 2006).

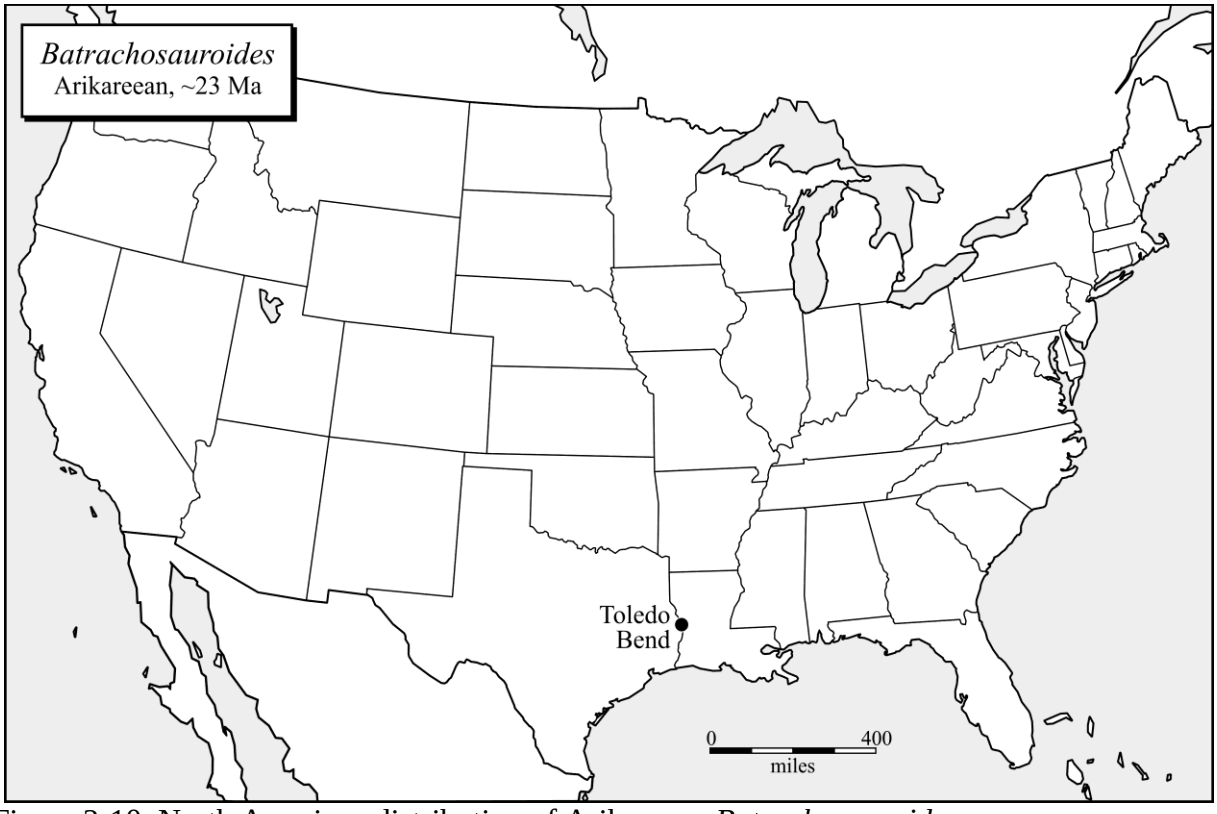

Figure 2-10. North American distribution of Arikareean *Batrachosauroides*.

During the Hemingfordian, *Batrachosauroides dissimulans* is known from the east Texas Oakville Formation and the Thomas Farm locality in central Florida (Figure 2-11; Holman, 2006).

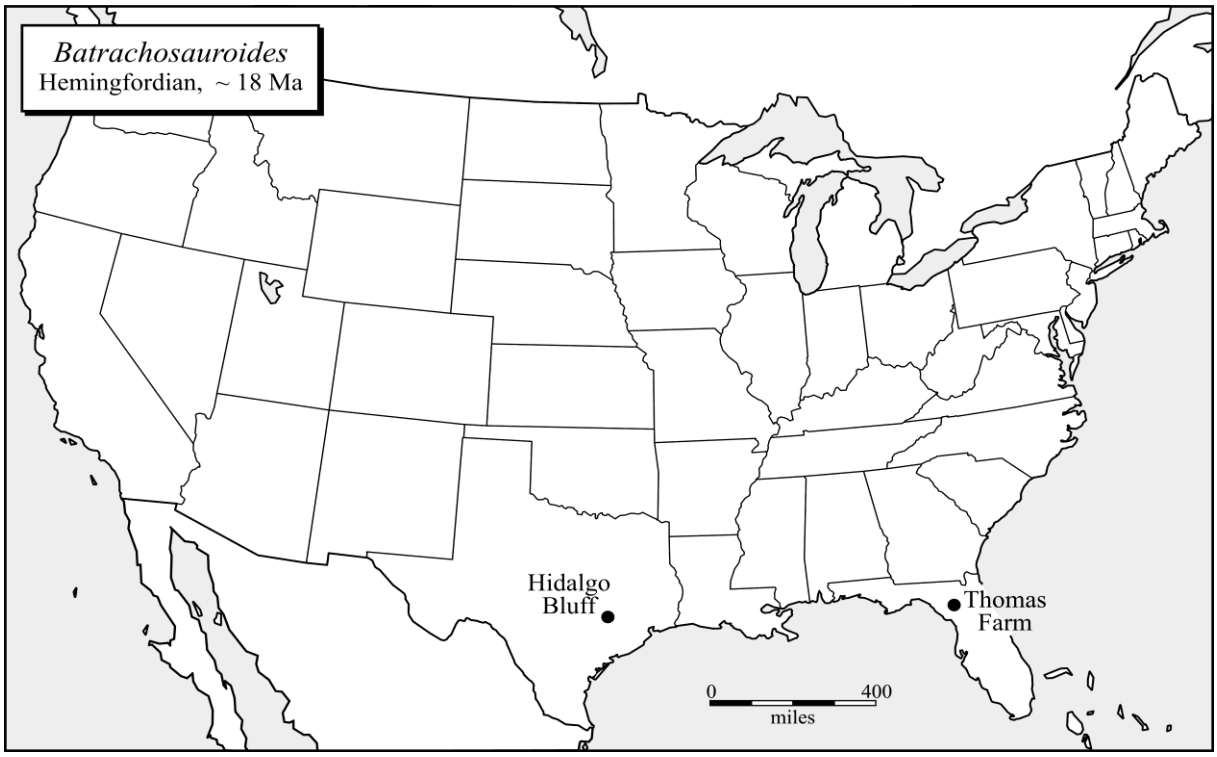

Figure 2-11. North American distribution of Hemingfordian *Batrachosauroides*.

By the early Barstovian, *Batrachosauroides dissimulans* was well documented from the Fleming Formation of eastern Texas, including records from several localities in San Jacinto and Polk counties and from the Florida Panhandle Willacoochee Creek locality (Figure 2-12; Taylor and Hesse, 1943; Auffenberg, 1958; Hinderstein and Boyce, 1977; Bryant, 1991; Holman, 2006). The late Barstovian TVOR *Batrachosauroides* represents the youngest occurrence of the genus in North America extending the temporal range by at least one million years (Figure 2-12).

Referral of LSUMG V-13858 to *Batrachosauroides* is based on the large size of the vertebra, the presence of the calcified cartilaginous ring on the condyle, and the large notochordal pit,

all of which are indicative of the Batrachosauroididae (Estes, 1969; Hinderstein and Boyce, 1977).

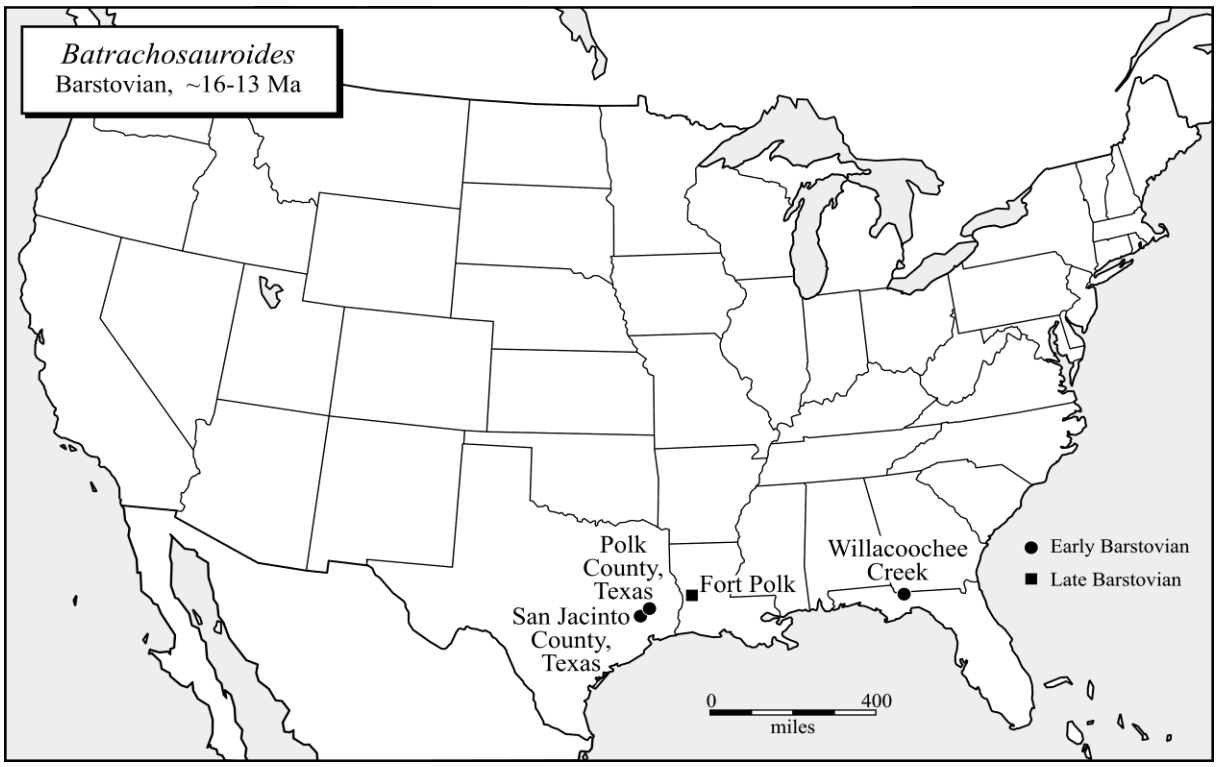

Figure 2-12. North American distribution of Barstovian *Batrachosauroides*.

The median keel of the Fort Polk vertebra is wider than those of *Batrachosauroides dissimulans* from the Willacoochee Creek fauna of the Florida panhandle (UF 111741), Gragg Mine, Georgia (UF 217589), and 13 vertebrae from Moscow Landing, Texas (SMPSMU 63672-13). It should be noted, however, that, of the 13 vertebrae examined from the Texas locality, there was much variation in this character that could be attributable to both intracolumnar or intraspecific differences. Auffenberg (1958) and Holman (2006) discussed intracolumnar variation and determined that the median keel is flatter and wider in the first few vertebrae posterior to the axis, so it is possible that LSUMG V-13858 is an anterior cervical vertebra.

Batrachosauroides dissimulans was first named as a new genus and species by Taylor and Hesse (1943) based on an articulated skull found in late Barstovian sediments (Cold Spring

Fauna) in San Jacinto County, Texas. Unfortunately, the skull has disappeared from collections. No associated vertebrae were found with the type skull, but Taylor and Hesse (1943) surmised that the vertebrae would have been amphicoelous rather than opisthocoelus, probably due to the occurrence of parasphenoid and splenial teeth on the type skull, allying it to the Amphiumidae, which have amphicoelous vertebrae (Auffenberg, 1958). Subsequently, Auffenberg (1958) referred several large opisthocoelus vertebrae collected near the type skull to *Batrachosauroides dissimulans* and erected the family Batrachosauroididae.

Class Amphibia Linnaeus, 1758

Order Caudata Oppel, 1811

Family, Genus and Species indeterminate

Referred material. ─ LSUMG V-13209, 10199, 13942, 13943, 13944,13945, 13946, 13947, 13948, 13949, 13950, eleven atlases from the Stonehenge site; LSUMG V- 13951, 13952, 13953, 13954, 13955, 13956, 13957, 13958, 13959, 13960, 13961, 13962, 13963, 13964, 13965, 13966, 13967, 13968, 13969, 13970, 13971, 13972, 13973, 13974, 13975, 13976, 13977, 13978, 13979, 13980, 13981, 13982, 13983, 13984, 13985, 13986, 13987, 13988, 13989, 13990, 13991, 13992, 13993, 13994, 13995, 13996, 13997, 13998, 13999, 20974, 20975, 20976, 20977, 20978, 21136, 21144, 21177, 21178, 21179, 21180, 21181, 21182, 21183, 21184, 21185, 21186, 21187, 67 fragmentary vertebrae from the Stonehenge site; LSUMG V-13134, 20939, 20981, 29982, 20983, 20984, 20985, seven fragmentary centra from the TVOR site, LSUMG V-20942, 20946, 20947, 10871, 20956, 20957, 20986 , seven atlases from the TVOR site; LSUMG V-20919, 20920, two atlases and LSUMG V- 20921, 20917, 20918, three fragmentary vertebrae from the TVOR SE site; LSUMG V-20931, one atlas from the TVOR North site; LSUMG V-20925, one

vertebral centrum from the TVOR North site; LSUMG V-20935, 20936, two fragmentary vertebral centra from the Discovery site.

Description. ─ Viewed dorsally the atlases are roughly pentagonal-shaped, and there is an odontoid process, which forms the apex of the pentagon. The neural arches are missing. Two anterior cotyles are present for articulation with the occipital condyles of the skull. Posteriorly, there is a single cotyle for articulation with the first trunk vertebra. Ventrally, the centrum is relatively flat, and there are two conspicuous subcentral foramina flanking the midline of the centrum. The fragmentary non-atlas vertebrae and vertebral centra are amphicoelous and bear subcentral foramina ventrally.

Discussion. ─ These vertebrae are all too fragmentary to identify to family or below at this time, as the differences between the specimens are very subtle. Salamander atlases have not been used in the identification of fossil salamanders and thorough comparisons of salamander atlas variation between families is necessary to determine if characters are present, that would aid in distinguishing taxa.

Superorder Salientia Laurenti, 1768

Order Anura Rafinesque, 1815

Fossil anuran bones are commonly recovered from localities that have been sieved, and Fort Polk and Tunica Hills/Kerry are no exception. Although radioulnae, humeri, tibiofibulae, and femora (Figure 2-13) are abundant frog postcranial bones at many localities, including Fort Polk and Tunica Hills/Kerry, their utility in making taxonomic determinations does not approach that of the ilium, which is also plentiful at vertebrate microsites, and has proven to be readily identifiable to the generic and sometimes specific level because of the abundance of diagnostic

characters (Figure 2-13) (Auffenberg 1956; Chantell, 1964; 1958; Holman, 1959, 1961, 1962, 1995, 2003). Finally, amphibian skull bones, including the tooth-bearing maxilla, frontoparietal, and squamosal, and the sacrum have been successfully used to identify fossil anurans (Holman, 2003).

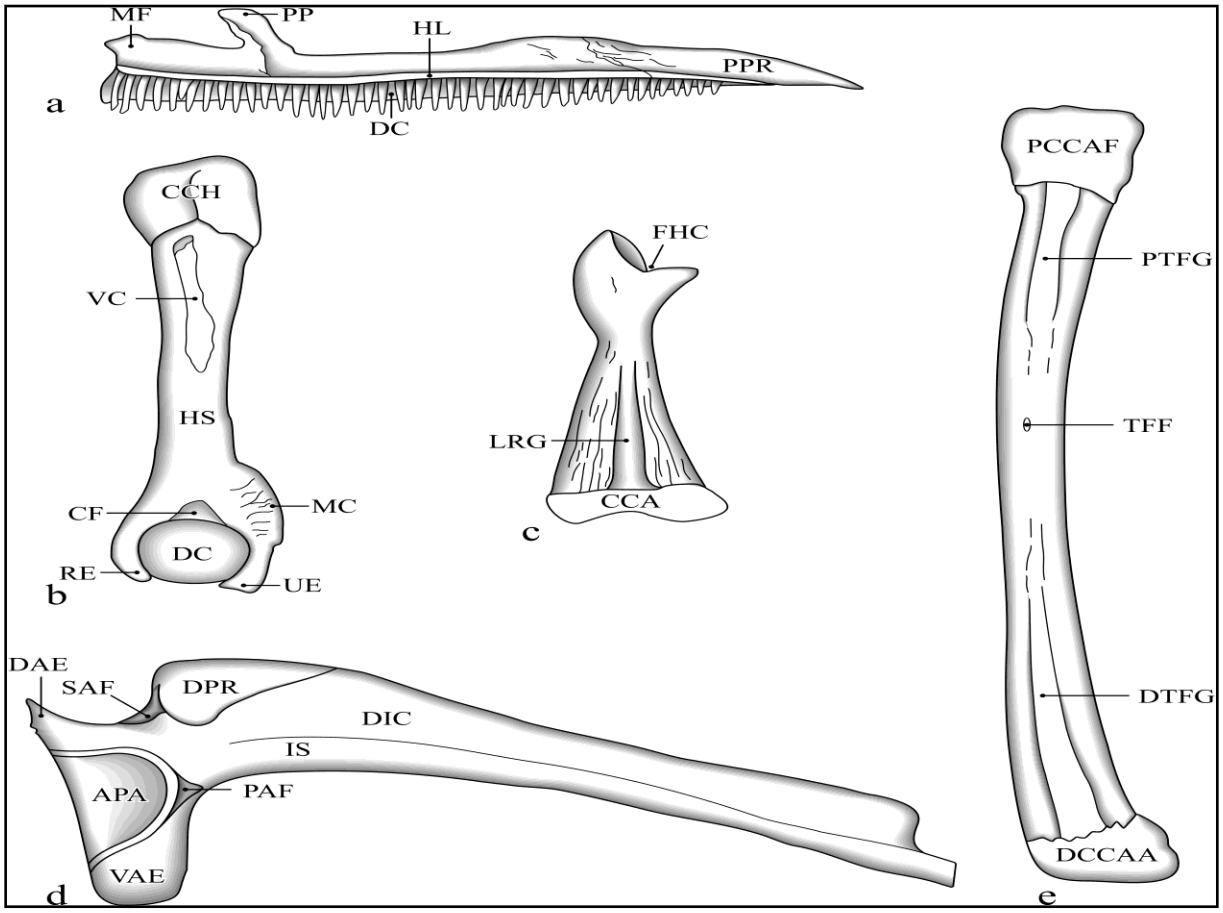

Figure 2-13. Important anuran bones used in the identification of fossil anurans. (a) Medial view of right maxilla: DC, dental crest; HL, horizontal lamina; MF, maxillary fossa; PP, palatine process; PPR, posterior process. (b) Ventral view of right humerus: CCH, calcified cartilaginous humeral head; CF, cubital fossa; DC, distal condyle; HS, humeral shaft; MC, mesial crest; RE, radial (lateral) epicondyle; UE, ulnar (medial) epicondyle; VC, ventral crest. (c) Lateral view of right radio ulna: CCA, calcified cartilaginous area for articulation with carpus; FHC, facet for distal condyle of humerus; LRG, lateral radio-ulnar groove. (d) Medial view of right ilium: APA, anterior portion of the acetabular fossa; DAE, dorsal acetabular expansion; DIC, dorsal ilial crest; DPR, dorsal prominence; IS, ilial shaft; PAF, preacetabular fossa; SAF, supra-acetabular fossa; VAE, ventral acetabular expansion. (e) Dorsal view of right tibiofibula: DCCAA, distal calcified cartilaginous area; DTFG, distal tibiofibular groove; PCCAT, proximal calcified cartilaginous surface for femur; PTFG, proximal tibiofibular groove; TFF, tibiofibular foramen. Modified from Holman (2003).

Family Hylidae Gray, 1825 (1815)

Genus *Acris* Dumeril and Bibron, 1841

Acris sp.

Figures 2-14, 2-15, 2-16, 2-17, 2-18, and 2-19

Referred material. ─ LSUMG V-13861, 13862, 13863, 13864, 13913, five left ilia from the Stonehenge site; LSUMG V-21149, one sacrum from the Stonehenge site; LSUMG V-13940, one right ilium and LSUMG V-13941, 20952, 21145, three left ilia from the TVOR site; LSUMG V-20924, one right ilium from the TVOR North Creek site.

Description. ─ The ilia are tiny and have a dorsal prominence that is long and low and blends smoothly into the dorsal ilial ridge. Atop the dorsal prominence is a laterally inflected dorsal tubercle that is ovoid and lies anterior to the anteriormost rim of the acetabular fossa by 50% of its length. The ilial shaft is relatively straight, and the ventral acetabular expansion is narrow, not extending anteriorly onto the ilial shaft.

LSUMG V-21149 is a diminutive procoelus sacrum with widely separated prezygapophyses and tubular sacral diapophyses that are directed slightly posteriorly. The condyles are round and well-separated. The centrum is dorsoventrally flattened and the cotyle is oval in shape

Discussion. ─ The first records of *Acris* in North America is that of the extinct species *Acris barbouri* from the Early Miocene (Hemingfordian) Thomas Farm locality in central Florida (Holman, 1967b; 2003) and an indeterminate *Acris* species from the Hemingfordian of Logan County, Colorado (Figure 2-17; Chantell, 1965; Holman, 2003). Middle Barstovian *Acris* have been reported from the Egelhoff local fauna in Keya Paha County, Nebraska (Holman, 1976e, 1987, 2003), the Norden Bridge local fauna in Brown County Nebraska, and the Fort Polk locality (Figure 2-18; Chantell 1964, 1966; Holman 1976; 2003). Finally, the Clarendonian

WaKeeney Local Fauna in Trego County, Kansas has produced *Acris* (Figure 2-19; Holman, 1975; 2003).

The small size, dorsal prominence position, and faint dorsal ilial ridge ally these ilia to *Acris*. Compared to modern *Acris crepitans* (specimen #'s LACM 16151, 162149, 162150, 162152, 162153) the ilial ridge of the Fort Polk specimens begins at the greatest dorsal height of the dorsal tubercle, smoothly blending the dorsal prominence and the ilial ridge; whereas, in the modern LACM specimens, there is a ventrally directed slope before the start of the ridge. Also, the ridge in the modern specimens is much more defined anteriorly than posteriorly, and more evident medially than laterally. Furthermore, there is a greater dorsoventral ilial shaft curvature in the modern LACM *Acris* specimens that is much less pronounced in the Fort Polk Stonehenge specimens. The dorsal tubercle of modern *Acris crepitans* and the Fort Polk specimens are similar in having a roughened surface and being oval-shaped.

The ilium of modern *Pseudacris ornata* (LACM 165171) has a dorsal tubercle that is not as anteroposteriorly expanded, is more medially conical than the Fort Polk ilia, and has a much greater dorsolateral curve. Furthermore, there is no dorsal ilial ridge present on LACM 165171.

Acris barbouri from the Hemingfordian Thomas Farm locality of Florida is the only named *Acris* species from the Miocene of North America. Not surprisingly, the Fort Polk *Acris* seem to share more characters with *Acris barbouri* than with any of the modern *Acris* specimens examined. For instance, Holman (2003) states that *A. barbouri* differs from modern *A. crepitans*, the northern cricket frog, from eastern North America and *A. gryllus*, the southern cricket frog, from the southeastern United States "in having (1) a low dorsal crest (ilial shaft ridge of some authors) gently arising from the anterior border of the dorsal prominence and having its dorsal margin straight (low crest arising well anterior to dorsal prominence and slightly curved dorsally

in *A. crepitans* and *A. gryllus*); (2) dorsal tubercle (dorsal protuberance of some authors) rounded and relatively smooth (dorsal tubercle oval and sometimes roughened in *A. crepitans* and *A. gryllus*); (3) ilial shaft almost straight (ilial shaft somewhat curved in *A. crepitans* and *A. gryllus*)". Interestingly, the Fort Polk *Acris* specimens share points one and three but not two with *Acris barbouri*; however, in his original description of the holotype, Holman (1967b) described the shape of the dorsal tubercle as ovaloid. If the Fort Polk *Acris* specimens prove to compare favorably to *Acris barbouri*, they may represent an intermediate form between modern *Acris* and *Acris barbouri*.

The sacrum has the well-separated condyles and prezygapophyses, diminutive size, and tubular sacral diapophyses characteristic of *Acris* (Chantell, 1968; Holman, 2003). It cannot be determined which *Acris* species the sacrum belonged to, as no Miocene sacra referable to *Acris* are known; however, the previously-mentioned characters are reasonable for reference of this specimen to the same taxon as the ilia.

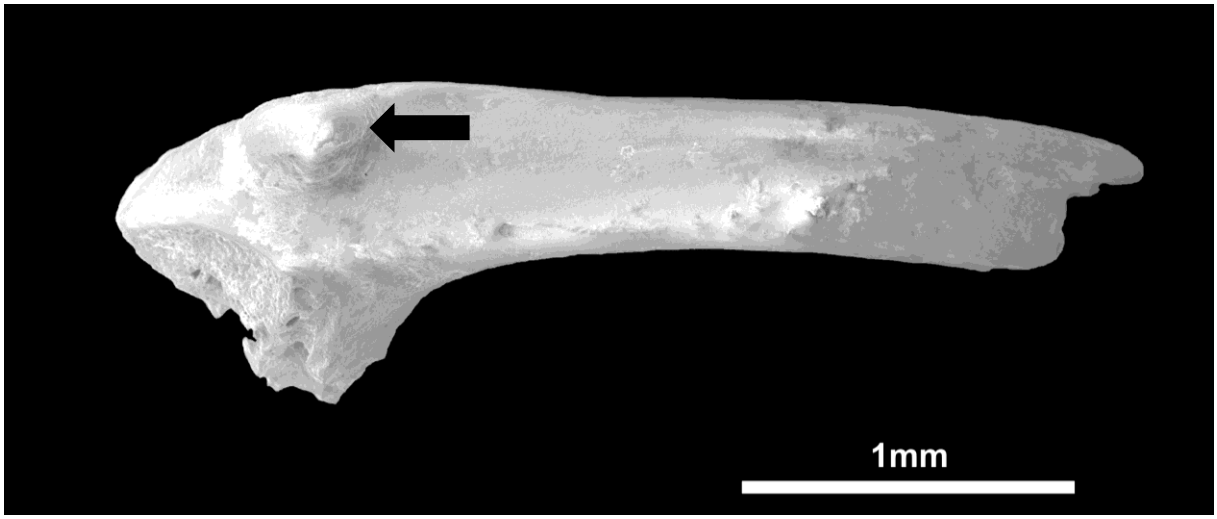

Figure 2-14. Scanning electron micrograph of *Acris* species indeterminate right ilium (LSUMG V-13861) in lateral view. The black arrow points to the anterior position of the dorsal prominence/protuberance.

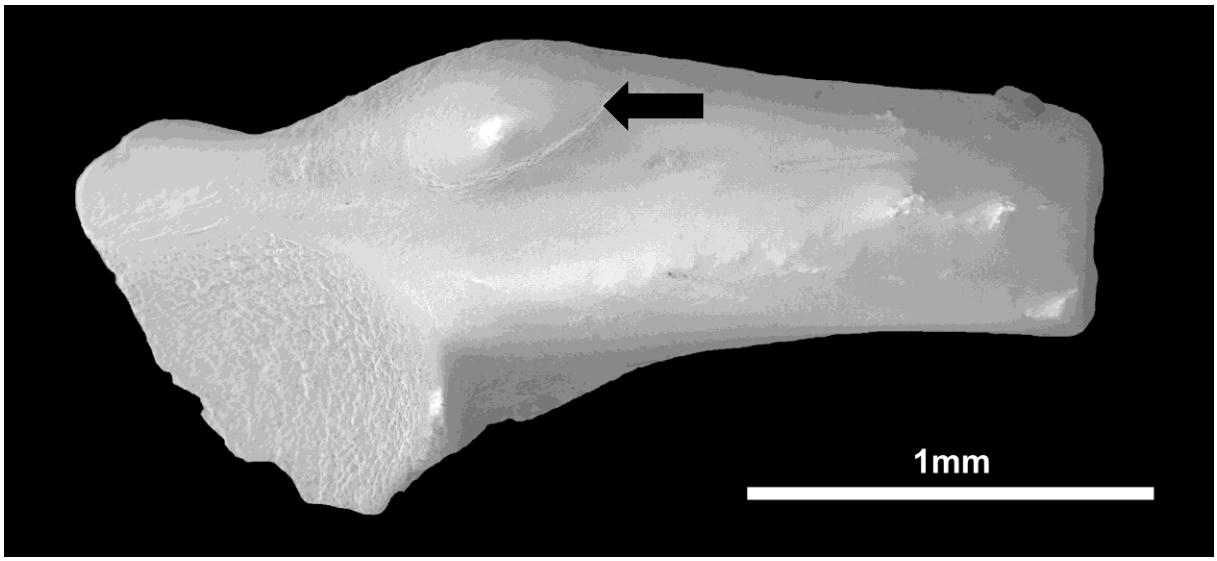

Figure 2-15. Scanning electron micrograph of *Acris* species indeterminate (LSUMG V-13940) right ilium in lateral view. The black arrow points to the anterior position of the dorsal prominence/protuberance.

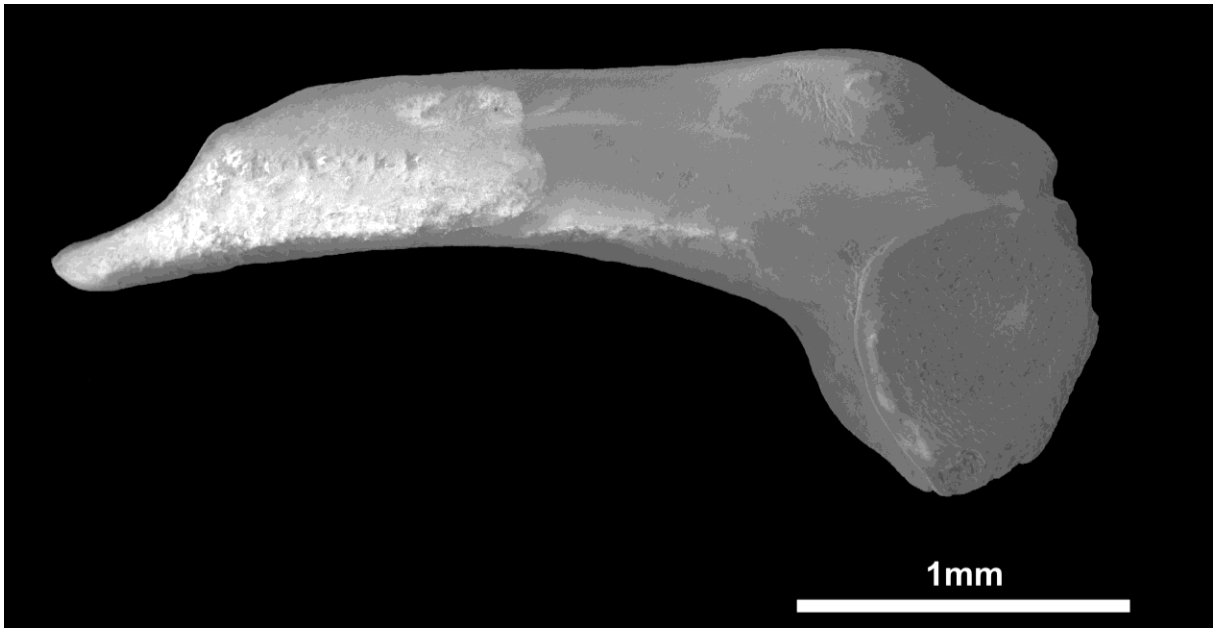

Figure 2-16. Scanning electron micrograph of *Acris* species indeterminate (LSUMG V-13862) left ilium in lateral view.

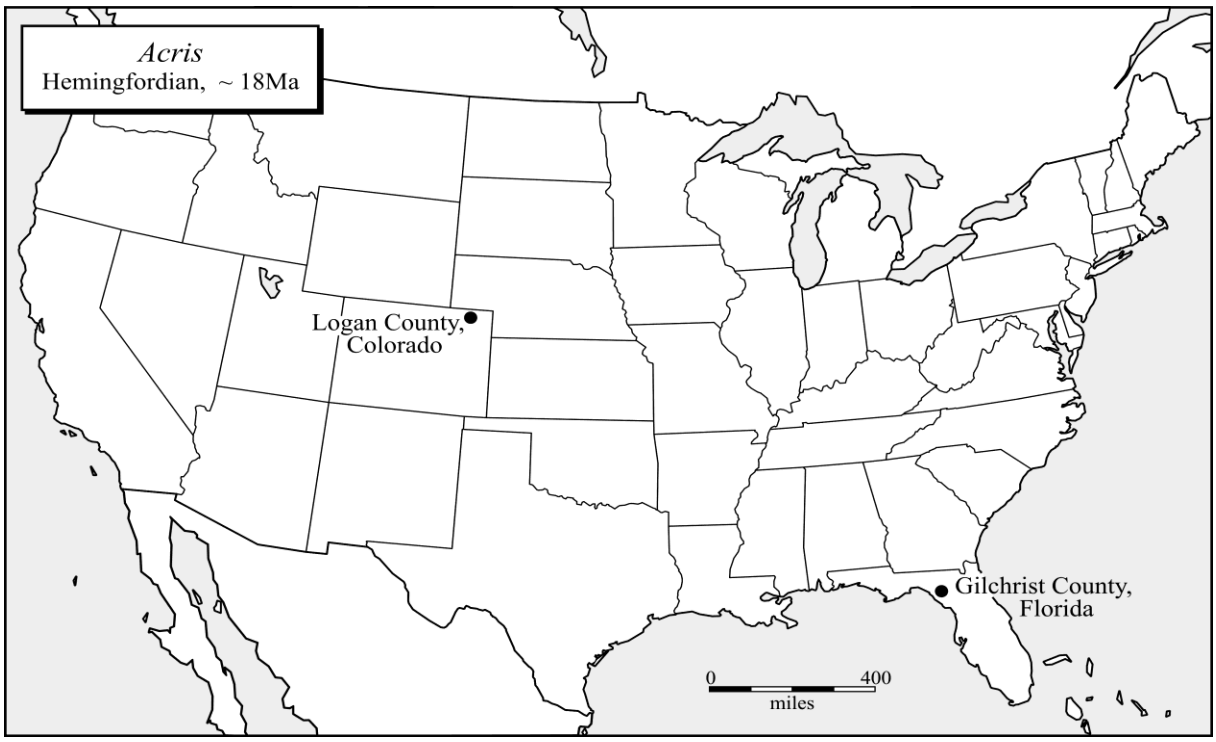

Figure 2-17. North American distribution of Hemingfordian *Acris*.

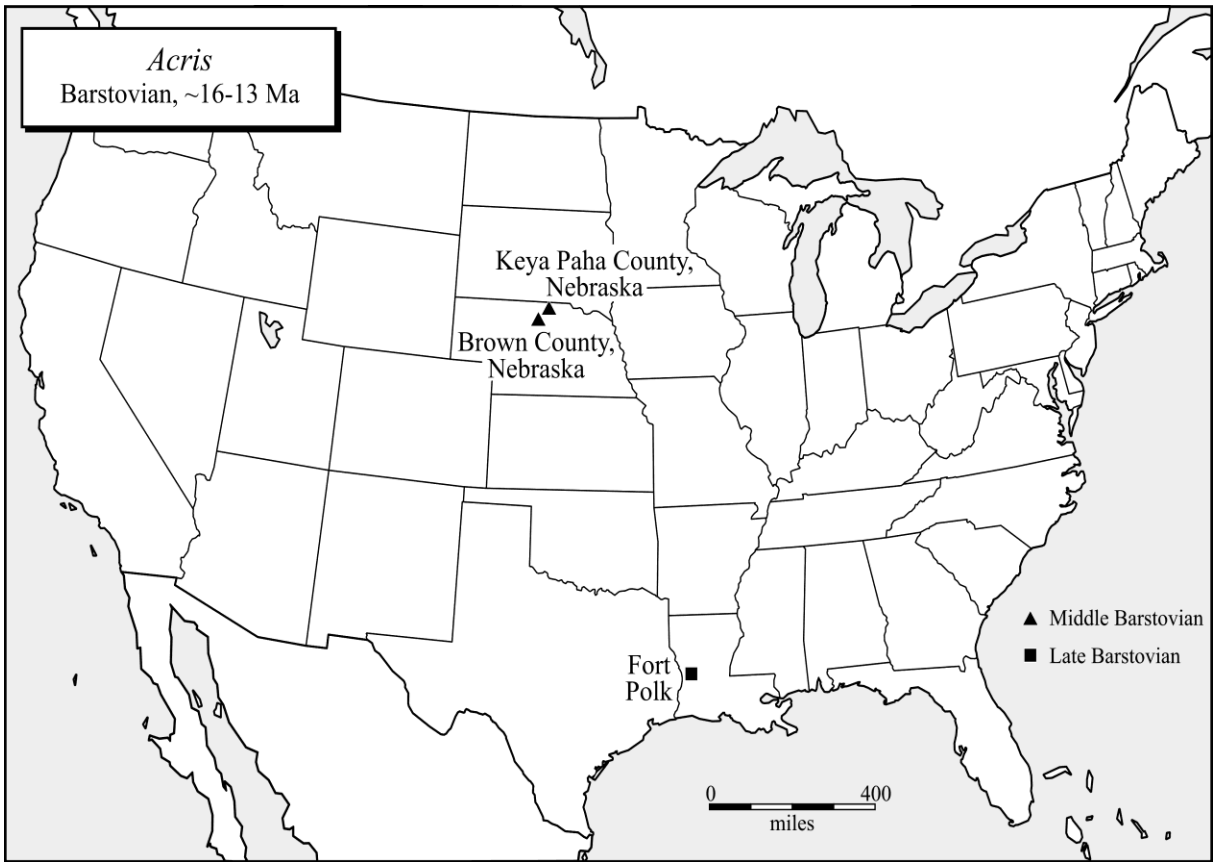

Figure 2-18. North American distribution of Barstovian *Acris*.

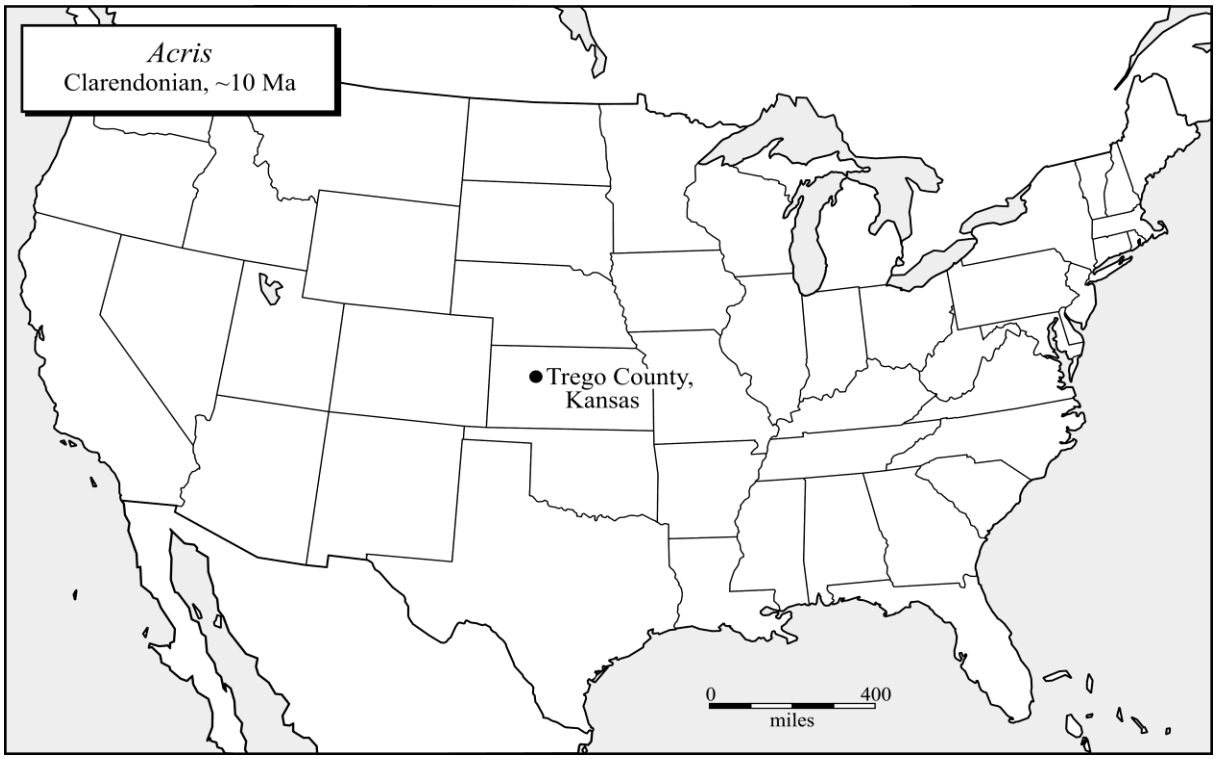

Figure 2-19. North American distribution of Clarendonian *Acris*.

Genus *Hyla* Laurenti, 1768

Hyla miocenica Holman, 1966

Figure 2-20 and 2-21

Referred material. ─ LSUMG V-21135, one left ilium from the Stonehenge site; LSUMG V-20963, one left ilium from the TVOR site.

Description. ─ The characters used to determine the taxonomic position of the Fort Polk ilia are as follows: 1) The dorsal prominence is weakly developed, 2) the dorsal tubercle produced dorsolaterally, 3) there is a wide angle between the ventral acetabular expansion and the ilial shaft, 4) the acetabular fossa is subtriangular-shaped, and 5) the ventral acetabular expansion is broad.

Discussion. ─ Prior to the discovery of the Fort Polk *Hyla miocenica* specimens, the holotype

ilium was the only specimen referred to the taxon, although, Holman (1977a) tentatively referred a hylid sacral vertebra to this species based on its small size. *Hyla miocenica* is only known from the early Barstovian of eastern Texas and the late Barstovian of Louisiana (Figure 2-21; Holman, 1977, 2003).

The sizes of the Fort Polk ilia are comparable to the holotype ilium. LSUMG V-21135 is more fragmentary than LSUMG V-20963, in having the dorsal tubercle missing, but compares well to the holotype in all other aspects. The dorsal tubercle of LSUMG V-20963 is more rounded and is positioned slightly anteriorly to the holotype ilium, which could be attributable to intraspecific variation.

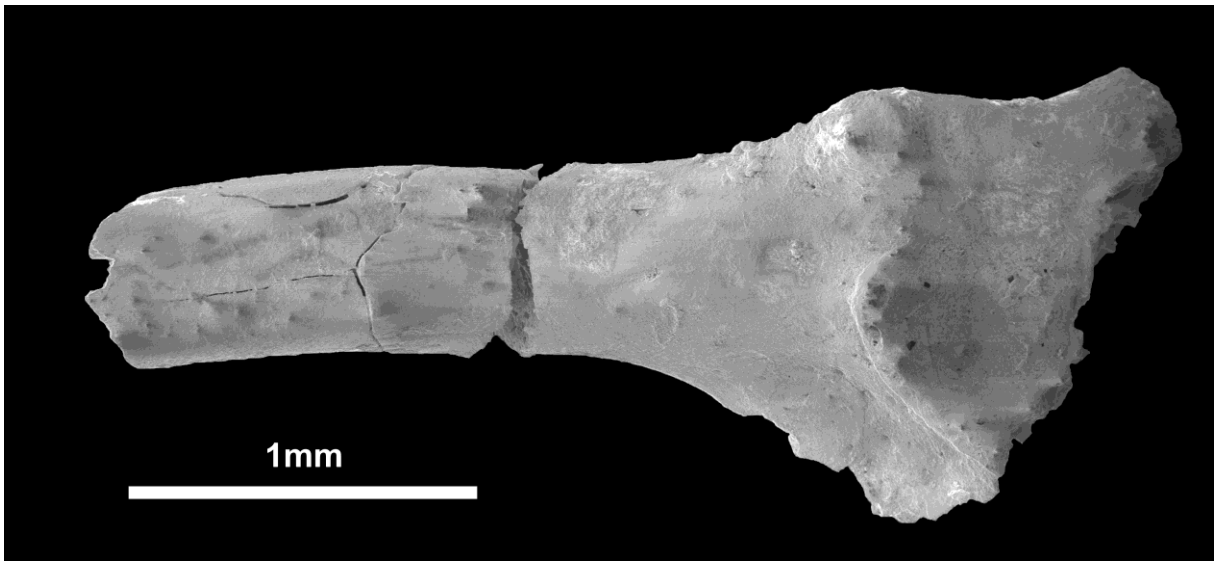

Figure 2-20. Scanning electron micrograph of *Hyla miocenica* left ilium in lateral view.

Genus *Hyla* Laurenti, 1768

Hyla sp.

Figures 2-22, 2-23, and 2-24

Referred material. ─ LSUMG V-20973, one left ilium from the Stonehenge site; LSUMG V-13859, V-13860, and V-20967 three right ilia from the Stonehenge site; LSUMG V-20937, one right ilium from the TVOR site; LSUMG V-13865, one right ilium from the Discovery site.

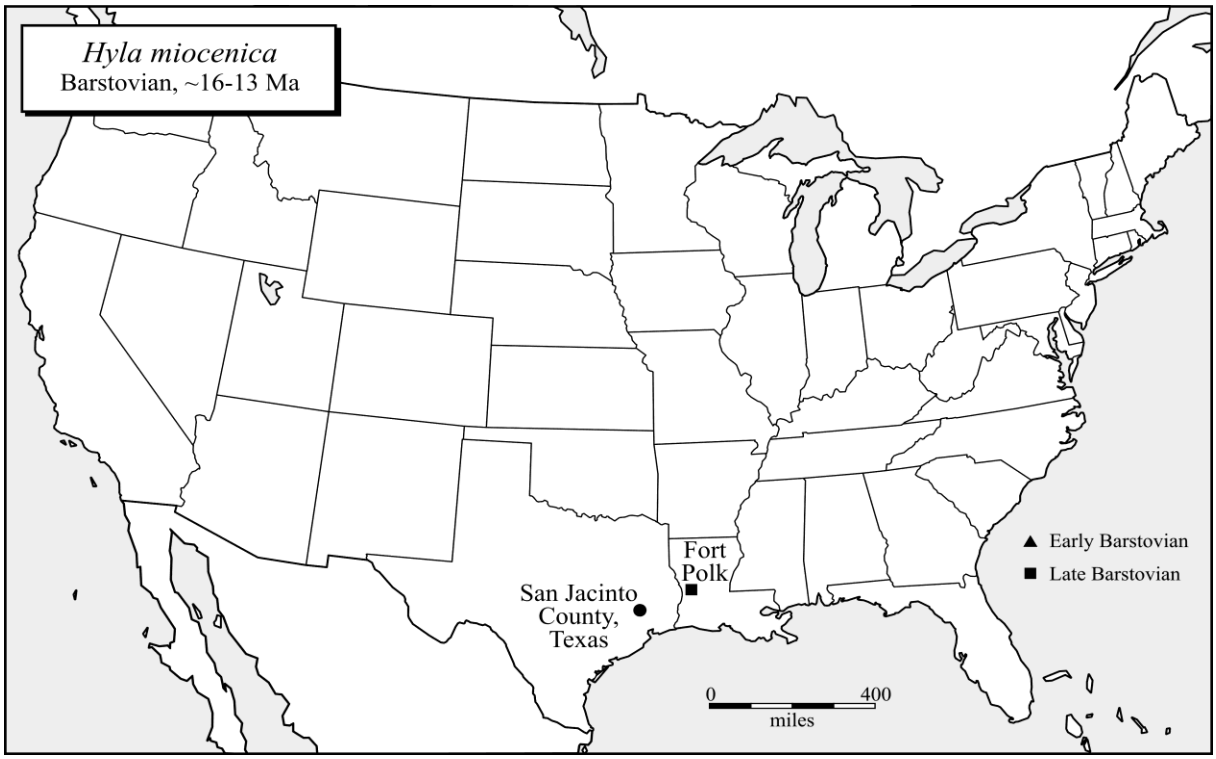

Figure 2-21. North American distribution of Barstovian *Hyla miocenica*.

Description. ─ All of these ilia are small and lightly built. LSUMG V-20973, 13859, 20967, and 13865 have oval-shaped dorsal tubercles that project dorsolaterally and are not very distinct from the dorsal prominence; whereas, LSUMG V-20937 has a dorsolaterally produced dorsal tubercle that is more rounded and distinct.

Discussion. ─ The small size and light build of these ilia, coupled with the dorsolateral projected dorsal tubercle, relate them to *Hyla* (Chantell, 1964). *Bufo* dorsal tubercles project dorsally (Auffenberg, 1957; Chantell, 1964), and *Rana* have dorsal ilial crests (Chantell, 1964; Holman, 2003).

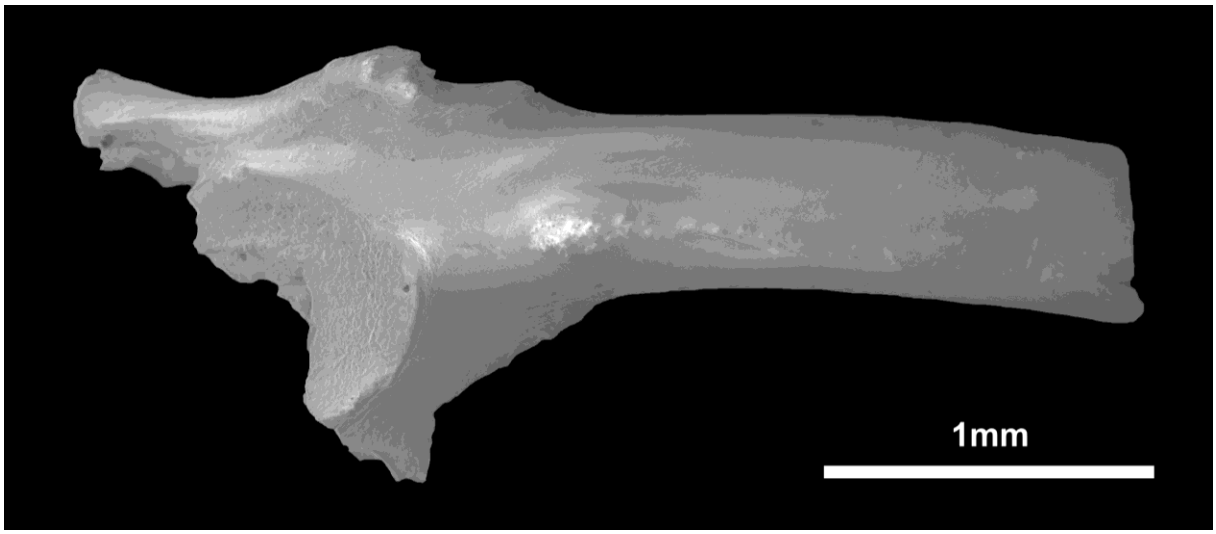

Figure 2-22. Scanning electron micrograph of *Hyla* species indeterminate (LSUMG V-13865) right ilium in lateral view.

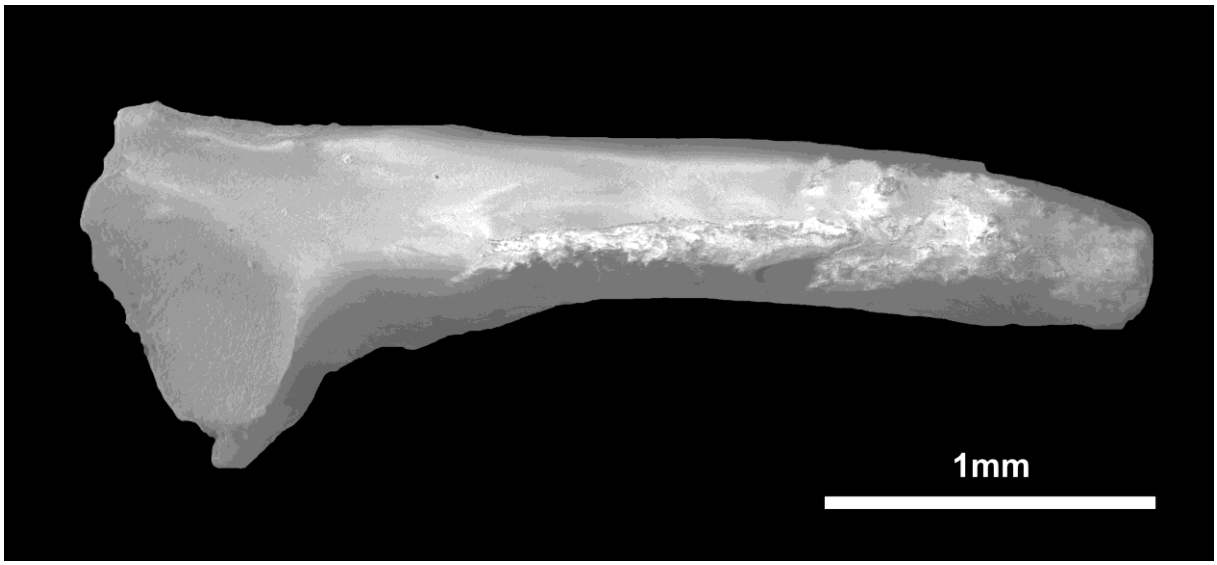

Figure 2-23. Scanning electron micrograph of *Hyla* species indeterminate (LSUMG V-13860) right ilium in lateral view.

Family Ranidae Gray, 1825

Genus *Rana* Linnaeus, 1758

Species indeterminate

Figures 2-24 and 2-25

Referred material. ─ LSUMG V- 13866, 13867, 13868, 13869, 13870,13871, 13872, 13873, 13874, 13875, 13876, 13877, 13878, 13879, 13880, 13881, 13882, 13883, 13884, 13897, 13912, 13235, 13222, 23 fragmentary left ilia from the Stonehenge site; LSUMG V-13885, 13886, 13887, 13888, 13889, 13890, 13891, 13892, 13893, 13894, 13895, 13896, 13213, 13223, 20962, 15 fragmentary right ilia from the Stonehenge site; LSUMG V-13898, V-20953, two fragmentary right ilia from the TVOR site; LSUMG V-20954, one fragmentary sacrum from the TVOR site; LSUMG V-12906, one fragmentary right ilium from the TVOR SE site; LSUMG V-20933, One fragmentary left ilium from the Discovery site.

Description. ─ These ilia are characterized by their moderate to large dorsal prominences and presence of a dorsal ilial crest on the ilial shaft. The acetabular fossa is not completely preserved in all of the ilia; the posterior portion is missing. Because of this, none of the ilia have a completely preserved ventral acetabular expansion. The ilial shaft is broken to some extent on all specimens, and no specimen displays a complete ilial crest. The area where the crest was broken, however, is readily apparent.

LSUMG V-20954 is a diplasiocoelus sacrum, having one condyle anteriorly and two condyles posteriorly. The posteriorly projecting condyles are widely separated. The neural arch is missing.

Discussion. ─ The designation of these ilia as *Rana* is based on the presence of moderate to large dorsal prominences and the presence of an ilial blade (Chantell, 1964; Holman, 2003). An ilial blade is also found in the Leptodactylidae, but it is not as pronounced as those in the Ranidae (Holman, 2003). Furthermore, ranid frogs have a more pronounced dorsal prominence and ilial blade. In his review of North American anurans, Holman (2003) stated the oldest leptodactylids are from the Irvingtonian of Texas. However, Holman (1967b) reported an indeterminate species of *Eleutherodactylus* from the Thomas Farm locality in Florida.

LSUMG V-20954 is extremely fragmentary but is designated *Rana* because of the diplasiocoelus condition of the sacrum (Holman, 1995).

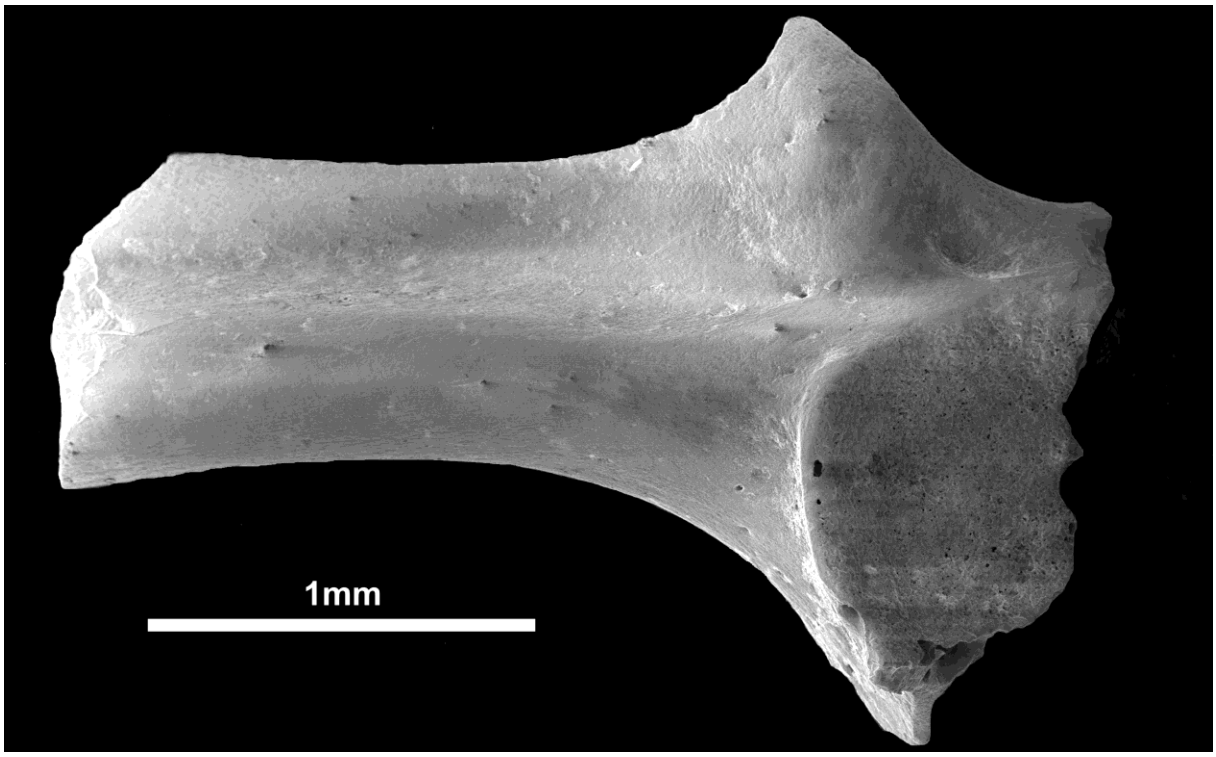

Figure 2-24. Scanning electron micrograph of *Rana* (LSUMG V-13866) left ilium in lateral view.

Superfamily Pelobatoidea Bolkay, 1919

Family Pelobatidae Bonaparte, 1850

Genus *Scaphiopus* (*Spea*) Holbrook, 1836

Schapiopus (*Spea*) sp. indeterminate

Figures 2-26 and 2-27

Referred material. ─ LSUMG V-21146, 21147, two fragmentary right ilia from the Stonehenge site.

Description. ─ These ilia have dorsal prominences that are long, low, and are produced dorsally slightly anterior to the anterior rim of the acetabulum.

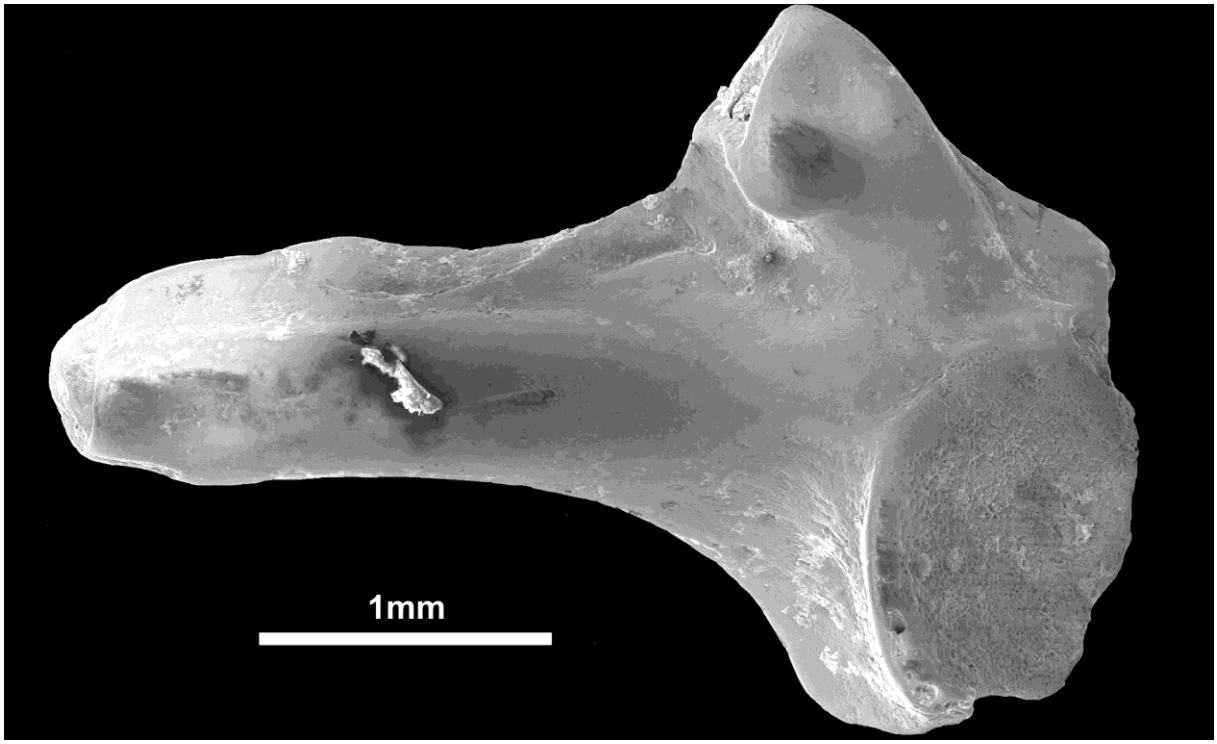

Figure 2-25. Scanning electron micrograph of *Rana* (LSUMG V-13881) left ilium in lateral view

LSUMG V-21146 has a ventral acetabular expansion that is slightly broader than LSUMG V-21147 and both extend slightly onto the ventral part of the ilial shaft. The ilial shaft of both specimens has a moderate curve. LSUMG V-21147 has a very shallow pre-acetabular fossa; whereas LSUMG V-21146 is more deeply excavated, but is still rather shallow.

Discussion. ─ These ilia are referred to the subgenus *Spea* based on their long low dorsal prominences that lack a dorsal tubercle. Holman (2003) stated two definitive osteological characteristics of *Scaphiopus* (*Spea*) *bombifrons* ilia are a reduced or absent dorsal prominence and no preacetabular fossa. The presence of the shallow preacetabular fossae in the Fort Polk specimens precludes their assignment to this species, but the ilia are more similar to *Scaphiopus* (*Spea*) *bombifrons* than to any other member of the subgenus. Kluge (1966) analyzed the variation in the amount of dorsal protuberance development in six species of *Scaphiopus* and

Scaphiopus (*Spea*) (Table 4 pg. 14 of Kluge (1966)) and found it to be range from absent to moderate in four out of six species. Given this variability, no specific determinations will be made at this time for the Fort Polk specimens.

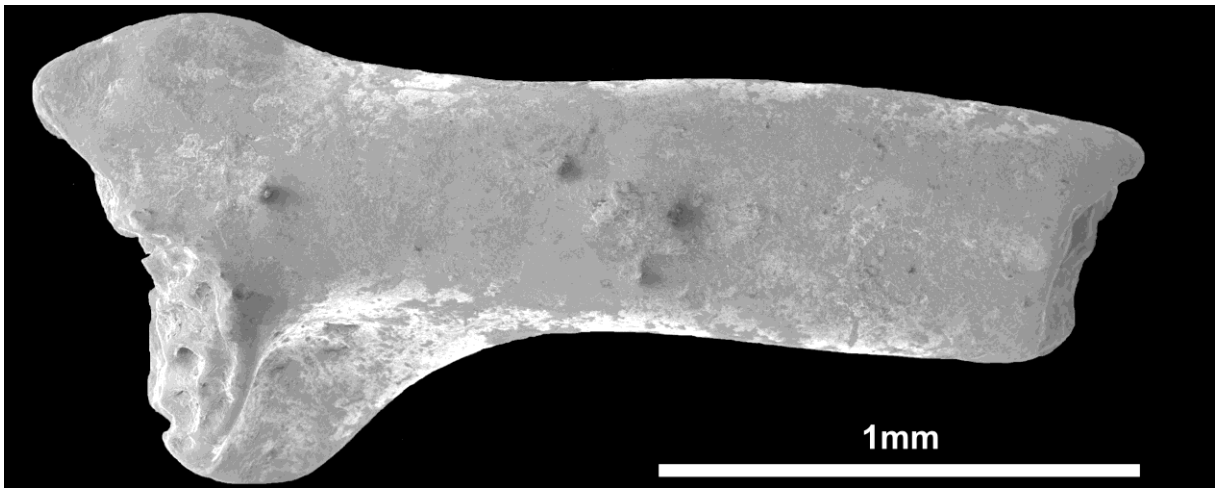

Figure 2-26. Scanning electron micrograph of ?*Scaphiopus* (*Spea*) (LSUMG V-21146) right ilium in lateral view.

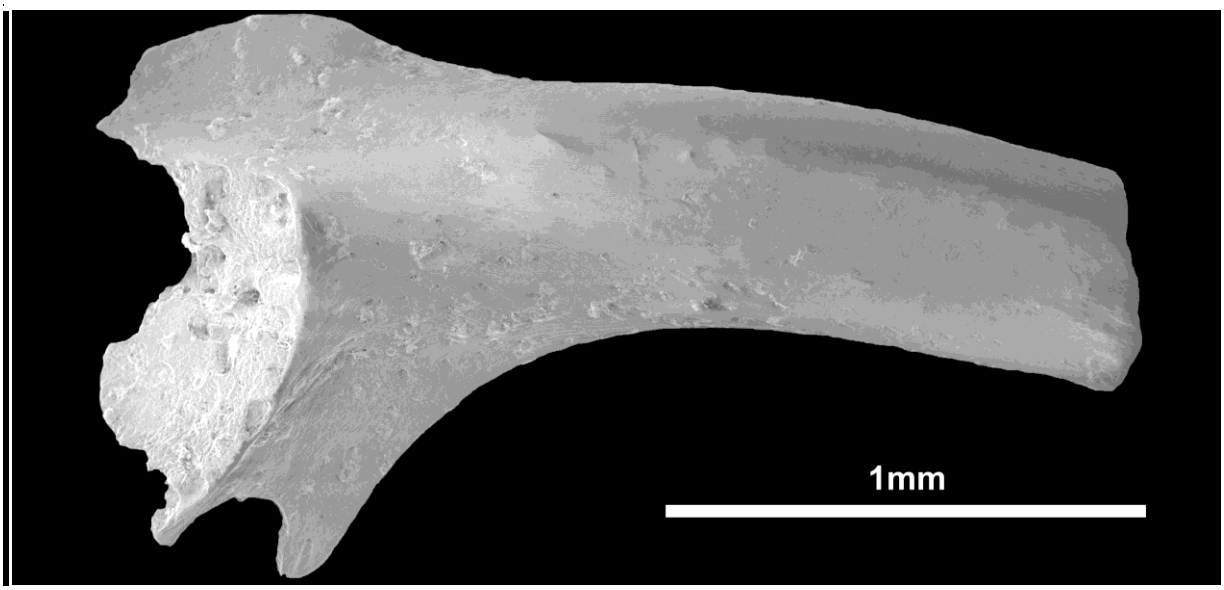

Figure 2-27. Scanning electron micrograph of ?*Scaphiopus* (*Spea*) (LSUMG V-21147) right ilium in lateral view.

Family Bufonidae Gray, 1825

Genus *Bufo*

Bufo cf. *Bufo hibbardi*

Figures 2-28, 2-29, 2-30, 2-31, and 2-32

Referred material. ─ LSUMG V-20964, one fragmentary left ilium from the Stonehenge site.

Description. ─ LSUMG V-20964 is broken both anteriorly and posteriorly, but has most of the acetabulum, ventral acetabular expansion, and dorsal prominence preserved. The dorsal prominence is produced dorsally, and is oriented anteromedially to the ilial shaft and has very little lateral displacement. The dorsal prominence is positioned anterior to the anterior edge of the acetabulum. The posterior slope of the prominence is smooth and not very vertical; whereas, the anterior slope is steep for the first third of its descent, then slopes much more gradually. There is a supra-acetabular fossa between the dorsal prominence and the broken dorsal acetabular expansion. The dorsal acetabular expansion projects posteriorly with almost no dorsal curvature, giving the expansion area a very narrow appearance. The ventral acetabular expansion is broad and extends onto the ilial shaft. There is a preacetabular fossa that defines the dorsal border of the expansion adjacent to the rim of the acetabulum.

Discussion. ─ *Bufo hibbardi* is an extinct species of toad that ranged from the middle Barstovian to the Hemphillian. Before the identification of *Bufo* cf. *Bufo hibbardi* from the Fort Polk locality, all Barstovian records were limited to Nebraska (Figure 2-30; Holman, 2003). The next occurrence is from the Clarendonian Wakeeney Local fauna in Trego County, Kansas (Figure 2-31; Holman, 1975, 2003). Finally, the Hemphillian occurrences are found in Keith County, Nebraska, and Sherman County, Kansas (Figure 2-32; Tihen, 1962; Parmley, 1992; Holman, 2003).

Bufo hibbardi is characterized by a dorsal prominence that has a gradual, smooth posterior slope and an anterior slope that slopes almost vertically then becomes more gradual (Holman, 2006). LSUMG V-20964 differs from *Bufo hibbardi* in the extreme anterior placement of the

dorsal tubercle and the oblique position of it in dorsal view.

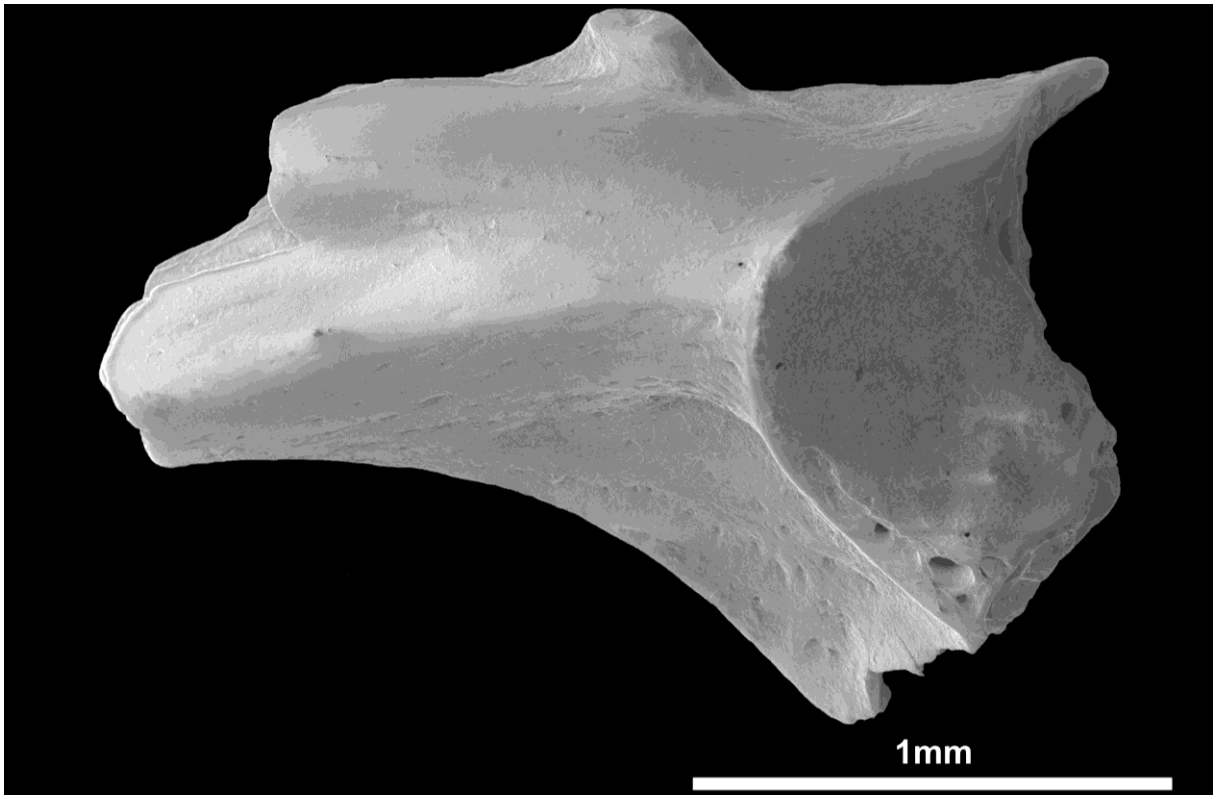

Figure 2-28. Scanning electron micrograph of *Bufo* species indeterminate (LSUMG V-20964) left ilium in lateral view.

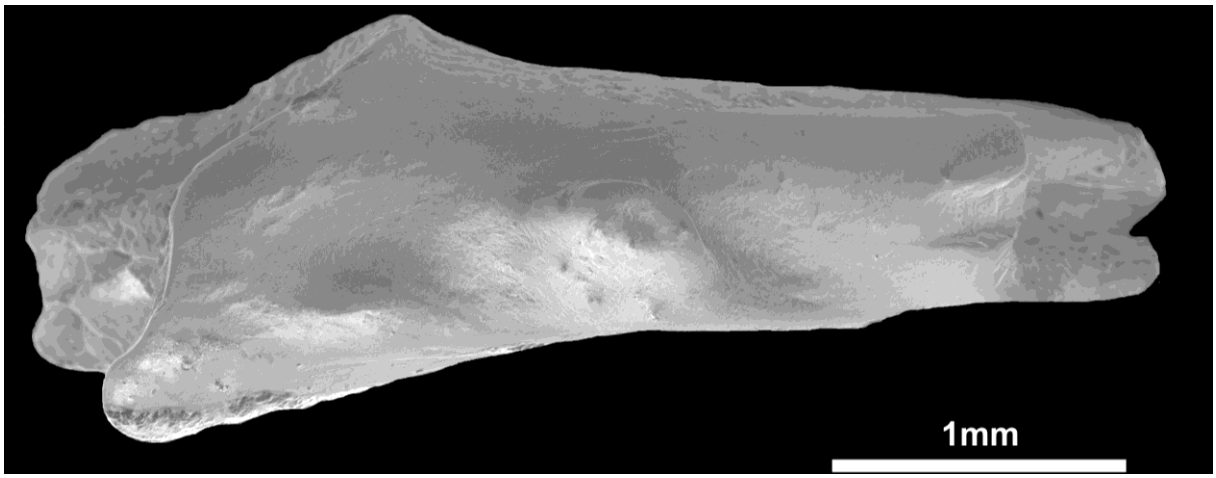

Figure 2-29. Scanning electron micrograph of *Bufo* species indeterminate (LSUMG V-20964) right ilium in dorsal view.

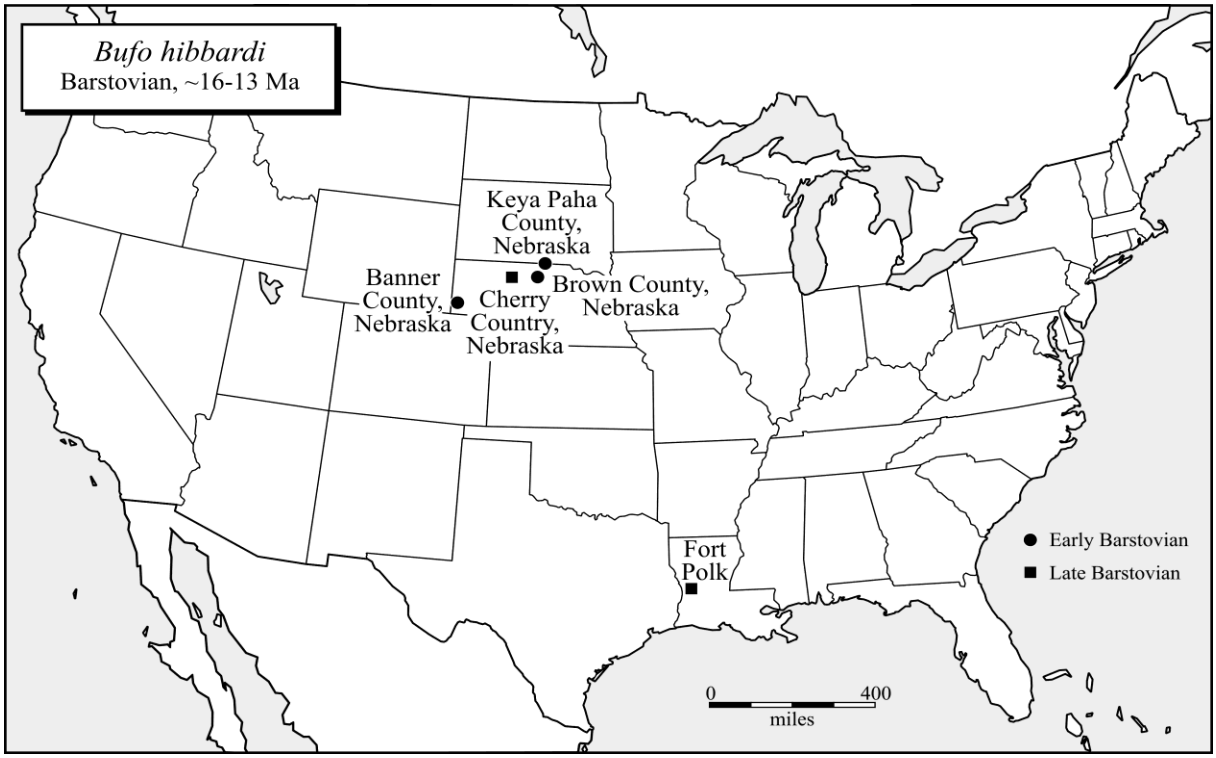

Figure 2-30. North American distribution of Barstovian *Bufo hibbardi*.

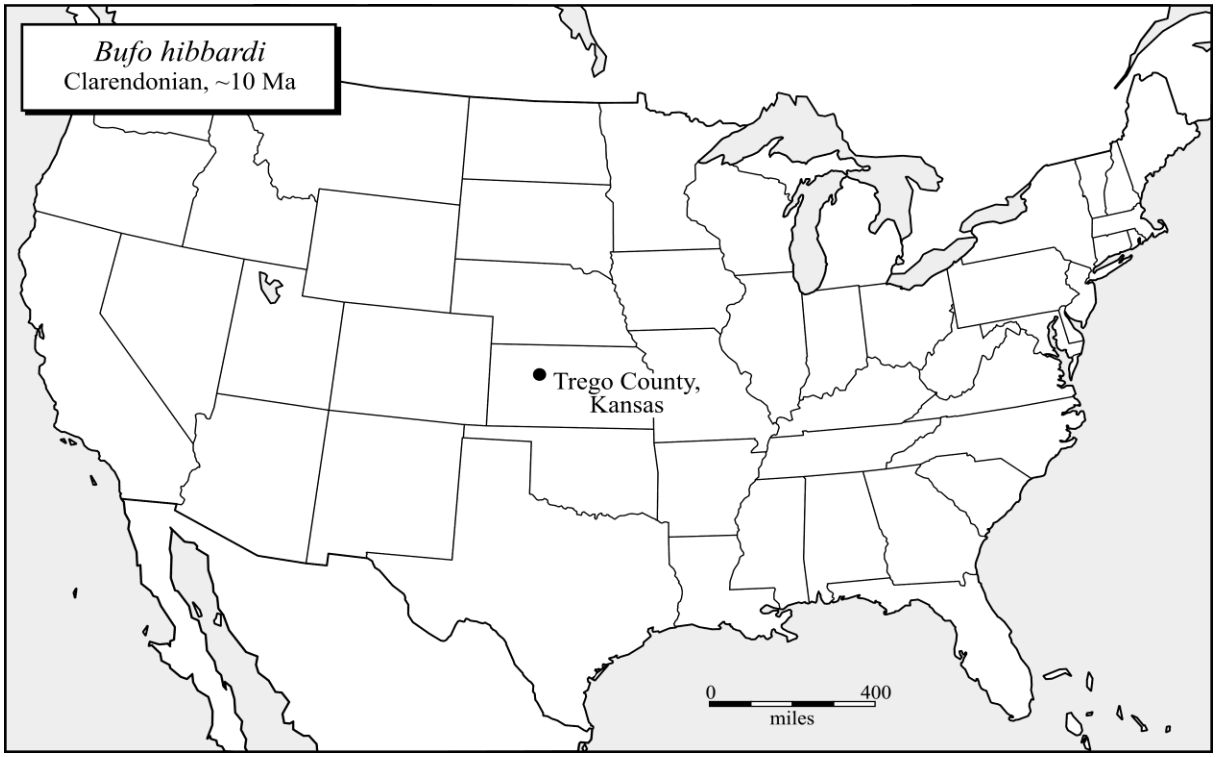

Figure 2-31. North American distribution of Clarendonian *Bufo hibbardi*.

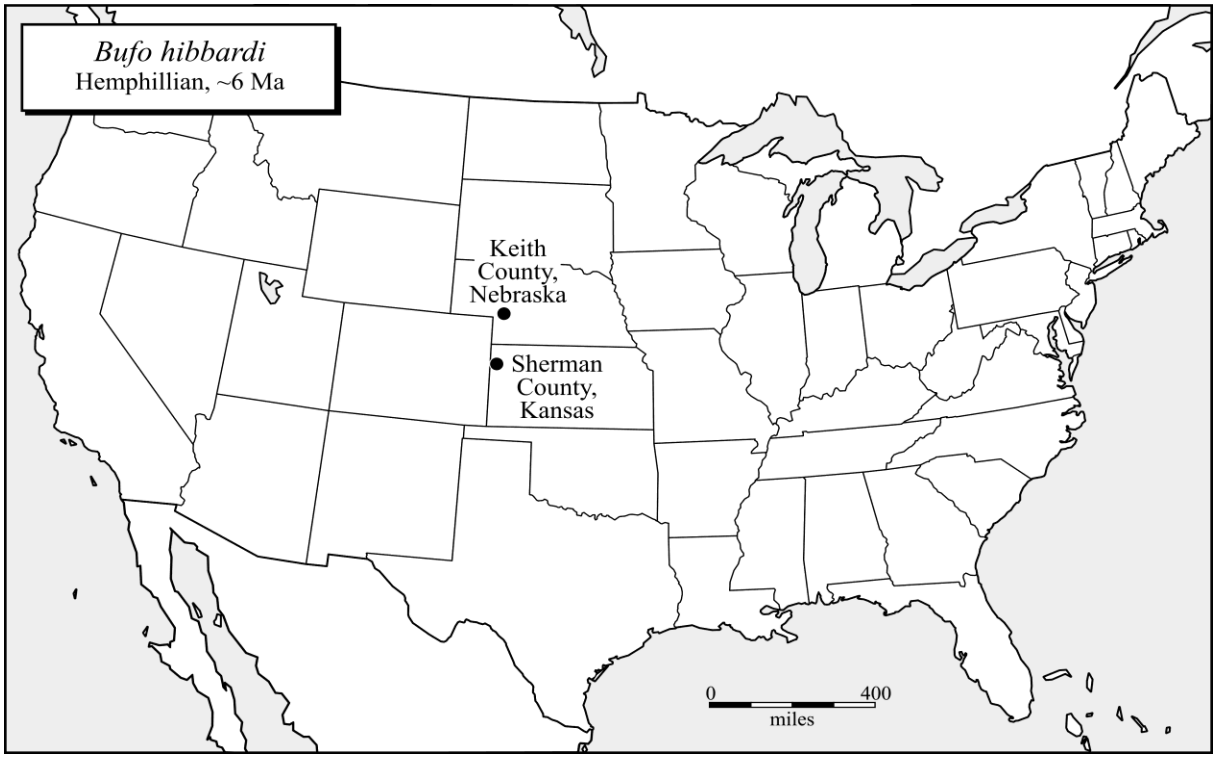

Figure 2-32. North American distribution of Hemphillian *Bufo hibbardi*.

Bufo Species indeterminate

Referred material. ─ LSUMG V- 20965, 20966, two fragmentary left ilia from the Stonehenge site; LSUMG V-3997, one fragmentary sacrum from the Stonehenge site.

Description. ─ LSUMG V-20965 and 20966 are small *Bufo* with long, low dorsally projected, dorsal prominences without the presence of tubercles. The anterior slope of the prominence on LSUMG V-20966 is slightly more gradual than the posterior slope. LSUMG V-20965 is slightly water-worn, having some areas somewhat rounded, but LSUMG V-20966 is better preserved. Both have narrow ventral acetabular expansions that are broken posteriorly.

LSUMG V-3997 is procoelus with an oval cotyle and oval condyles. The centrum is flattened dorsoventrally. Most of the sacral diapophyses are missing. The area preserved is slightly expanded.

Discussion. ─ The long, low dorsally projected dorsal prominence of LSUMG V-20966 is unlike any I have seen thus far. LSUMG V-20965 is too worn and rounded to determine a species. LSUMG V-3997 was described *cf. Bufo* in Schiebout and Ting (2001) and they determined it to be similar to modern *Bufo valliceps*.

Anuran Family, Genus, and Species indeterminate

Referred material. ─ LSUMG V- 20968, 20969, 20970, 20971, 20972, 21159, 21160, 21161, 21162, 21163, ten fragmentary ilia from the Stonehenge site; LSUMG V-21148, 21150, 13212, 21171, four fragmentary sacra from the Stonehenge site; LSUMG V-4971, one nearly complete vertebra from the Stonehenge site; LSUMG V-21151, 21152, 21153, 21154, 21155, 21156, 21157, seven vertebral centra from the Stonehenge site; LSUMG V- 20938, 20948, 20949, three anuran vertebrae, LSUMG V- 20940, 21175, two sacra from the TVOR site; LSUMG V-12797, One ilium and LSUMG V-20932, one anuran vertebral centrum, from TVOR North site; LSUMG V-21225, 21226, two fragmentary centra from the TVOR Southeast North Wall site; LSUMG V-10832, one sacrum from the TVOR North Creek site.

Description. ─ The ilia are all fragmentary with most of the ilial shaft and dorsal prominences not preserved. The sacral and pre-sacral vertebrae are procoelus with dorsoventrally flattened centra but are mostly fragmentary with the neural arches missing.

Discussion. ─ Unfortunately the above listed ilia are too fragmentary to make any taxonomic determinations other than anuran, as key diagnostic features such as the dorsal prominences/tubercles and the ilial blades are not preserved. Presacral vertebrae are not used much in anuran identifications, and with the exception of LSUMG V-4971, which is mostly complete, the other vertebrae mostly consist of centra with the neural arches missing. Likewise,

the sacra are too fragmentary to identify because of a lack of preservation of neural arches and sacral diapophyses, which are important diagnostic characters.

Anuran Family, Genus, and Species indeterminate

Referred material. ─ LSUMG V-13899, 13901, 13902, 13903, 13905, five distal left humeri from the Stonehenge site; LSUMG V-13900, 13904, 20960, three distal right humeri from the Stonehenge site; LSUMG V-13906, 13907, 13908, 13909, 20950, five distal left humeri from the TVOR site; LSUMG V-13910, 13911, 20943, 20944, 20945, 20951, 20955, seven distal right humeri from the TVOR site; LSUMG V-20930, one distal right humerus from the TVOR North site; LSUMG V-20922, one distal right humerus, LSUMG V-20923, one distal left humeral ball from TVOR North Creek site; LSUMG V-20928 and 20929, two fragmentary right humeri from the TVOR North Creek site;.

Description. ─ LSUMG V-13899 is a moderate sized anuran humerus, and is well-preserved with little indication of wear. The distal condyle is prominent and rounded. The radial (lateral) epicondyle is present but reduced in size, possibly due to wear. The medial (ulnar) epicondyle is prominent and flares out from the distal condyle. The medial epicondyle is rounded when viewed laterally, following the outline of distal condyle. The cubital fossa is present. There is a mesial crest present along the medial side of the humeral shaft and the beginning of a ventral crest that is truncated by the broken end of the shaft.

From LSUMG V-4967 is a small anuran humerus that is broken proximally, such that the ventral crest is not preserved. The medial (ulnar) epicondyle is weakly developed, but this may be partly due to wear, as the surface is roughened and pitted under high magnification.

Discussion. ─ LSUMG V-4633 A differs from *Bufo valliceps* humeri in having a more rounded

distal condyle (oval in *Bufo valliceps*), and rounded ulnar epicondyle when viewed laterally. The large mesial crest is indicative of a male anuran and is used during amplexus.

Unfortunately, anuran humeri are not commonly used postcranial elements in the identification of fossil anurans. Whether this is due to intraspecific variability as proposed by Holman (2003) or lack of rigorous osteological comparisons of modern taxa, needs to be determined.

Anuran Family, Genus, and Species indeterminate

Referred material. ─ LSUMG V-13914, 13915, 13916, three proximal urostyle fragments from the Stonehenge site.

Description. ─ These urostyle fragments have broken dorsal prominences and urostylar crests, but well-preserved cotyles.

Discussion. ─ The urostyle is a bone unique to anurans that contributes to the formation of the reinforced pelvic girdle that articulates with the condyles of the sacral vertebra and aids in the powerful jump of frogs (Holman, 2003; Pough, 2001). Although there are differences in overall cotylar shape and cotylar margins, the fragmentary nature of the dorsal prominences and urostylar crests, coupled with the lack of published data on using anuran urostyles for taxonomic determinations of fossil taxa, precludes their use for identification at this time. Further studies on urostylar morphologic variability of modern taxa needs to be conducted before their utility in determining taxonomic affinities can be ascertained.

Anuran Family, Genus, and Species indeterminate

Referred material. ─ LSUMG V-13917, 13918, 13919, 13920, 13921, 13922, 13923, 13924,

13925, 13926, 13927, 13928, 13929, 13930, 13931, 13932, 13933, 13934, 20958, 20959, 21168, 21169, 20934, 23 proximal ends of radio-ulnae from the Stonehenge site; LSUMG V-13936, 13937, 13938, 13939, four proximal ends of radio-ulnae from the TVOR site. LSUMG V-20926, one fragmentary proximal radio-ulnar end from the TVOR N. Creek site.

Description. ─ These specimens are small to medium in size and exhibit the characteristic facet for the humeral condyle, which is a smooth 90° curve. The shaft of most of these specimens is broken before the midway point; therefore the lateral radio-ulnar groove is not visible.

Discussion. ─ The anuran radio-ulna is the fused lower front limb element. Proximal radio-ulnae are frequently found in sieved sites, as they are durable and resistant to degradation; however, they are not used to identify fossil anurans because of a lack of viable characters (Holman, 2003), and as such will be left as anuran indeterminate in this report.

Anuran Family, Genus, and Species indeterminate

Referred material. ─ LSUMG V-21166, one tibiofibula from the Stonehenge site; LSUMG V-20941, 20961, two tibiofibulae from the TVOR site.

Description. ─ These tibiofibulae are recognized by the fusion of the tibia and fibula, which can be seen in the proximal and distal tibiofibular grooves. The grooves are the fusion line between the two bones. Tibiofibular foramina are also present in dorsal, and sometimes, ventral views.

Discussion. ─ Other than size, no trenchant character differences are evident between the Fort Polk tibiofibulae. Holman (2003) stated that the tibiofibular foramen is present on the dorsal surface of the tibiofibula. LSUMG V-21166 from the Stonehenge site and LSUMG V-17952 from the Tunica Hills/Kerry site display tibiofibular foramina on the dorsal and ventral surfaces

that are slightly offset from each other. Further studies are necessary to determine if this character state is found in all anurans, or if it arises only in certain taxa.

Class Reptilia Laurent, 1768, emend. Gauthier, Kluge, and Rowe, 1988

Order Chelonia

Suborder Cryptodira

Superfamily Trionychoidea

Family Trionychidae Meylan, 1987

Referred material. ─ LSUMG V-3883, two carapace fragments from the Discovery site.

Description. ─ LSUMG V-3883 consists of two carapace fragments with characteristic pitted pattern on the dorsal surface.

Discussion. ─ Schiebout (1997) described this specimen and determined it lacked diagnostic characters to assign it to species. Since Schiebout (1997) more trionychid shell material has been recovered, but the material is no more diagnostic than LSUMG V-3883.

Superfamily Testudinoidea

Family Testudinidae

Genus *Hesperotestudo*

Species indeterminate

Referred material. ─ LSUMG V-12223, 12224, two complete tortoise carapaces and plastrons from the Discovery site.

Description. ─ These tortoises consist of two almost complete articulated carapaces and

plastrons. The ventral surface of the plastron of LSUMG V-12223 is slightly concave, whereas, LSUMG V-12224 is flatter. Both specimens have octagonal-shaped second and third neural bones of the carapace (Schiebout *et al*., 2004).

Discussion. ─ The genus *Hesperotestudo* has been synonomized with *Geochelone* in North America (Robert McCord, *Pers. Comm*., 2003; Schiebout *et al.*, 2004). *Geochelone* has second and fourth neural bones that are octagonal in outline, which separates them from *Stylemys* and *Hadrianus* (Schiebout *et al.*, 2004).

Order Crocodylia

Family Crocodylidae

Genus *Alligator* sp.

Referred material. ─ LSUMG V-3888, Alligator teeth from the TVOR site.

Description. ─ Small alligator type teeth with blunt tips, giving them a rounded appearance in lateral view. There are faint dorsoventral striations extending from the apex of the crown to the base.

Discussion. ─ Schiebout (1997) described these teeth as *Alligator* sp. because mandibular symphyses or splenial bones have not been recovered from Fort Polk and these bones contain characters that are useful in making specific determinations. It is unfortunate that isolated crocodilian teeth have not been useful in diagnosing taxa, as Fort Polk has several distinct morphologies.

Order Squamata Oppel, 1811

Suborder Alethinophidae Nopcsa, 1923

North American fossil snakes are usually described using morphological characters of isolated trunk vertebrae, as the majority are not found articulated (Holman, 2000, 2006). When presented with isolated anuran remains, the ilium has proven to be the most diagnostic element (Holman, 2003). Diagnostic bones of fossil lizards, on the other hand, are the mandible, maxilla, premaxilla, and isolated osteoderms.

Snake vertebrae are complex structures with well-developed pre and postzygapophyses, neural spines, and hypapophyses or hemal keels in derived taxa (Figure 2-33). All postcranial snake movements are supported by vertebrae and ribs only (Holman, 1995). Snake vertebral complexity allows researchers to identify fossil taxa using suites of characters illustrated in Figure 2-33.

It is widely recognized that snake the vertebral column displays intraspecific, interspecific, ontogenetic, and intracolumnar variation (Holman, 1979, 1981b, 1995, 2000; LaDuke, 1991). The problem of snake vertebral variability can be overcome when large comparative collections of modern and fossil taxa are available and the fossil specimen in question is fairly complete; however, distinguishing between some genera, such as *Masticophis* and *Coluber* is exceedingly difficult (Holman, 2000).

The elongate snake morphology necessitates large numbers of vertebrae, ranging in modern taxa from 141 to 435 total vertebrae and up to approximately 565 in the Eocene taxon, *Archeophis* (Romer, 1956). The large number of vertebrae in individual snakes partially account for the commonness of isolated snake vertebrae in many Neogene deposits, especially where large amounts of sediment have been screened.

The trunk vertebrae are particularly diagnostic to the familial and generic levels and sometimes to the specific level (Holman, 2000, 2006).

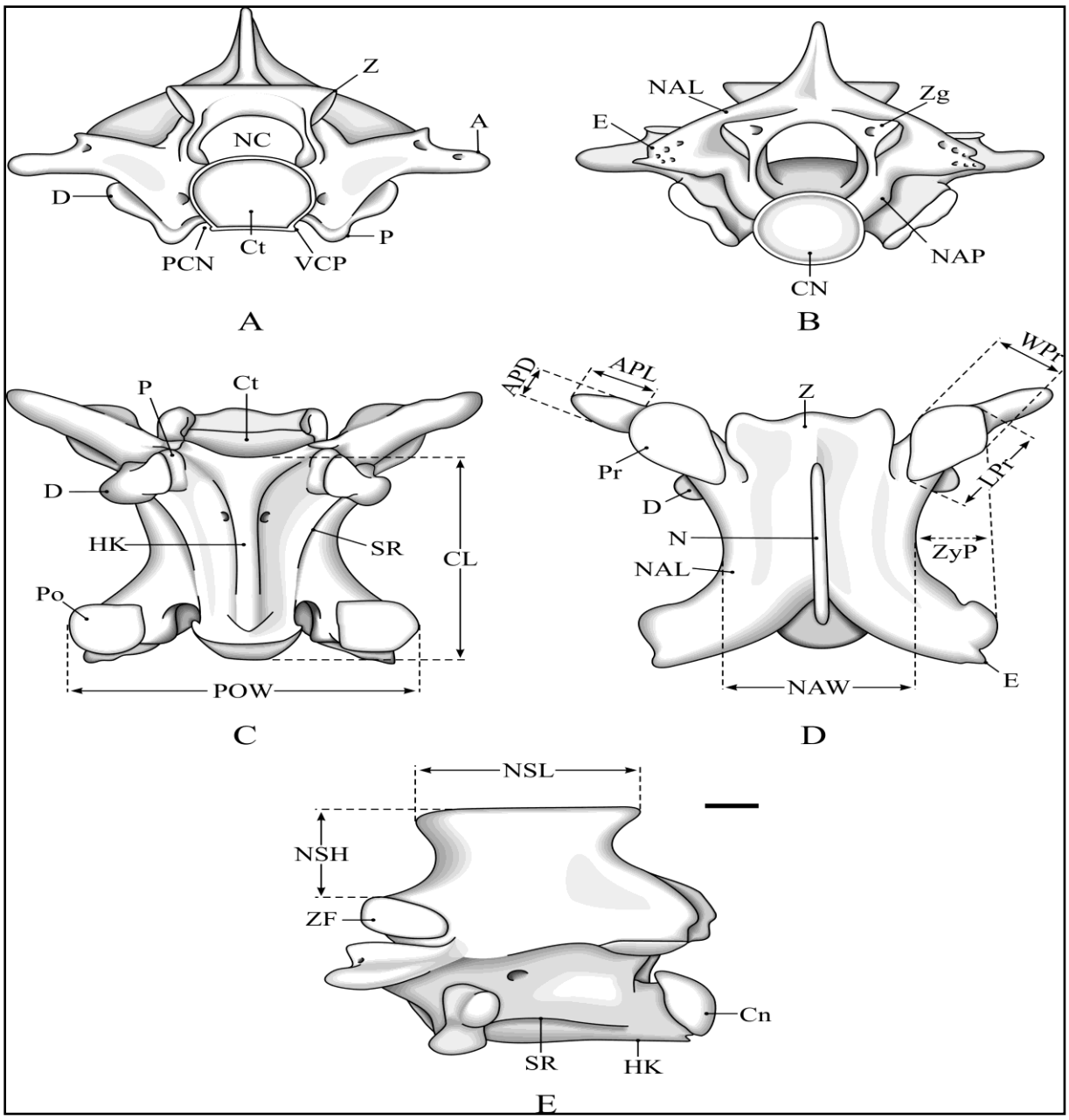

Figure 2-33. Colubrine MTV in A.anterior, B. posterior, C. ventral, D. dorsal, and E. lateral views: A, accessory process; APD, accessory process diameter; APL, accessory process length; CL, centrum length; Ct, cotyle; Cn, condyle; D, diapophysis; E, epizygapophyseal spine; HK, hemal keel; LPr, prezygapophysis length; N, neural spine; NAL, neural arch lamina; NAP, neural arch pedicel; NAW, neural arch width; NC, neural canal, NSH, neural spine height; NSL, neural spine length; P, parapophysis; PCN, paracotylar notch; Po, postzygapophyseal articular facet; POW, width across postzygapophyses; Pr, prezygapophyseal articular facet; SR, subcentral ridge; VCP, ventrolateral cotylar process; WPr, width of prezygapophysis; Z, zygosphene; ZF, zygosphenal facet; ZG, zygantrum; ZYP, greatest lateral distance between the neural arch and outer edge of the zygapophyses. Modified from LaDuke (1991). Scale bar is equal to one mm.

The snake vertebral column has been subdivided differently by various authors and different terminology employed for the various regions (Auffenberg, 1963; Holman, 1979, 2000; LaDuke, 1991). This study will recognize a combination of the vertebral regions used by LaDuke (1991) and Holman (2000), namely, anterior trunk vertebrae (ATV) (cervical vertebrae), middle trunk vertebrae (MTV), posterior trunk vertebrae (PTV), cloacal vertebrae, and caudal vertebrae. The ATV region does not include the atlas and axis, which thus far, have not been identified in the Louisiana herpetofaunas described in the following sections. When unable to distinguish between MTV and PTV, due to the subtlety of intracolumnar changes, "trunk vertebra" will be the descriptive term used.

All ATV have posteriorly-projecting hypapophyses, originating from the ventral surface of the centrum (Auffenberg, 1963; Holman, 1979, 2000; LaDuke, 1991). In colubrine and boid snakes, hypapophyses are replaced by a hemal keel or nothing at all, as one transitions from ATV to MTV and PTV; whereas viperid and natricine snakes retain their hypapophyses throughout the ATV, MTV, and PTV regions. Hypapophysis and hemal keel shape are important characters used in the identification of fossil snakes and will be discussed more thoroughly in the systematic paleontology section. Determining whether a snake vertebra is a natricine trunk vertebra or an ATV, can be difficult; however, ATV differ from MTV and PTV in the following ways: 1) ATV have a larger neural canal and smaller condyle, 2) the lateral extent of the zygapophyses is limited, and 3) the vertebrae are dorsalventrally elongated and anteroposteriorly reduced (Holman, 1979, 1981b; Rage, 1988; LaDuke, 1991).

Superfamily Booidae Gray, 1825

Family Boidae Gray, 1825

Subfamily Boinae 1825

Genus *Boavus* Marsh 1871

Boavus cf. *Boavus affinis* Brattstrom, 1955

Figure 2-34

Referred material. ─ LSUMG V-21129, one trunk vertebra from the TVOR SE site; LSUMG V-21130, one fragmentary neural arch from the Gully site.

Description. ─ LSUMG V-21129 is massively built and is wider than long. Viewed dorsally, the neural spine extended anteriorly well onto the zygosphene. The zygosphene is concave and does not flair much. The zygantrum and posterior portion of the neural is spine is missing. The prezygapophyses are too worn to determine the shape. Viewed laterally, the synapophyses are wide, long, and prominent. The centrum is short. The interzygapophyseal ridge slopes downward anteriorly. Viewed ventrally, the centrum is short, wide, and triangular-shaped. An indistinct, wide hemal keel is present, and the postzygaphophyseal articular facets are too worn to ascertain the shape. Viewed posteriorly, the condyle and the neural canal are subtriangular in shape, and the neural arch is extremely thickened compared to a comparably-sized colubrid vertebra. Viewed anteriorly, the cotyle appears to have been subtriangular-shaped. There are distinct paracotylar foramina flanking the cotyle that do not reside in well-excavated fossae. The prezygapophyses are slightly tilted upward. The massive zygosphene is dorsoventrally thickened and dorsolaterally narrowed.

LSUMG V-21130 is a partial vertebra and consists of the remains of most of a neural arch with a slightly worn zygosphene that is concave when viewed dorsally, dorsoventrally thickened, and dorsolaterally narrowed. The zygosphenal and zygantral articular facets are massive. The neural spine is broken, but extended onto the zygosphene. The cotyle is missing, but there are

two foramina present lateral to where the cotyle would be, which probably are paracotylar foramina.

Discussion. ─ *Boavus affinis* was a wide ranging (both geographically and temporally) boine snake that is not well-documented in the fossil record. It first appears in the Middle to Late Eocene Sespe Formation in southern California (Brattstrom, 1955; Holman, 2000). There are no occurrences of this taxon between the Late Eocene and the early Barstovian of Texas, where Holman (1996) identified a vertebra as ?*Boavus affinis* based on the overall shape, neural spine morphology, and presence of paracotylar foramina (Figure 2-34). The late Barstovian record from Fort Polk, Louisiana, is the youngest occurrence of this taxon (Figure 2-34).

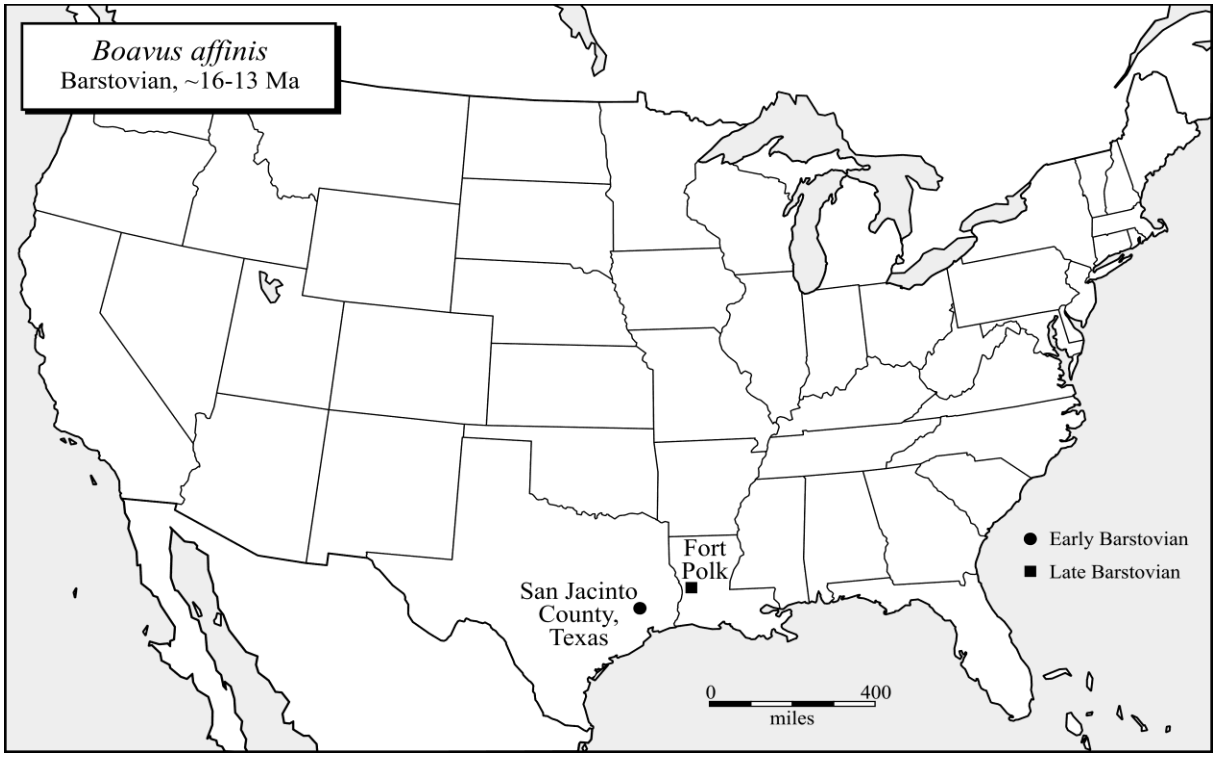

Figure 2-34. North American distribution of Barstovian *Boavus affinis*.

Modern boine snakes include the familiar pythons and boas of the new and old world tropics and subtropics (Holman, 2000). At first glance, the massiveness of these vertebrae is readily

apparent. The assignment of LSUMG V-21129 and 21130 to the subfamily Boinae is based on the following: 1) overall vertebral shape is short and wide, 2) the zygosphene is dorsoventrally thickened compared to those of colubrid, viperid, and elapid snakes, 3) the centrum is extremely triangular-shaped, and 4) the synapophyses are massive (Holman, 2000).

Comparisons of LSUMG V- 12314 with *Boavus affinis* from NHMLAC (CIT 180**)** reveals the following: *Boavus affinis* from California has a much more pronounced hemal keel and the presence of subcentral ridges and grooves; the hemal keels are similar in the dorsoventral thickness and concave edge; the neural spines of *Boavus affinis* and LSUMG V-12314 extend well onto the zygosphene. Both taxa share the wide vertebral morphology, paracotylar foramina, and triangular shape of the centrum.

Miocene records of boine boids on the Gulf Coast are rare. Holman (1977; 1996; 2000) described an indeterminate boine from early Barstovian Livingston Dam site in east Texas, and Holman (1996; 2000) described a specimen of ?*Boavus affinis* from the early Barstovian Trinity River locality also in east Texas. This determination was based on the prominent neural spines of *Boavus affinis* from the early Arikareean Sespe Formation in California, which are also present on the Texas specimen, and the presence of paracotylar foramina, a trait not seen in other species of *Boavus* (Holman, 1996; 2000). The presence of paracotylar foramina on the Louisiana specimens allies them with *Boavus affinis*.

It is interesting to note that these records of boids in the late Barstovian of Louisiana represent the last records of the subfamily Boinae on the entire Gulf Coast. Bryant (1991) hypothesized that the boids were extirpated from the southeastern US by the early Barstovian, as he noted the lack of boids from the early Barstovian Willacoochee Creek Fauna. Similarly, Holman (2000)

noted the early Barstovian records from Texas as representing “the last gasp of the subfamily Boinae east of the continental divide in North America”.

Boine Genus and Species indeterminate

Referred material. ─ LSUMG V-21290, one trunk vertebra from the Stonehenge site.

Description. ─ From the dorsal view, LSUMG V-21290 has a wide zygosphene and a poorly developed, dorsoventrally short, wide neural spine . The posterior portion of the neural arch, including the zygantrum, is missing, as are the pre- and postzygapophyses. In lateral view the synapophyses are massive and the neural spine is obsolete. It has a short, wide centrum with a distinctly wide hemal keel when viewed ventrally. In lateral view the synapophyses are massive and the neural spine is dorsoventrally short. Posteriorly, the neural arch is dorsoventrally thickened and vaulted and, the condyle is subtriangular-shaped. Anteriorly, the cotyle is oval, the zygosphene is slightly dorsoventrally thickened, and is slightly wider than the cotyle.

Discussion. ─ This vertebra is worn, with most sharp edges rounded. It is referred to the boinae because of the short, wide, triangular form of the centrum; the large synapophyses; and the dorsoventrally thickened zygosphene. It is believed that the diminutive but wide neural spine is the result of breakage and wear during the burial process.

Subfamily Erycinae Bonaparte, 1831

Genus *Calamagras* Cope, 1873

Calamagras sp.

Referred material. ─ LSUMG V-21191, one trunk vertebra from the TVOR site.

Description. ─ This small vertebra is very wide with a depressed neural arch, a neural spine that is short and low, and a short centrum with a distinct, wide hemal keel flanked by fairly deep subcentral grooves. The cotyle is subtriangular. The right prezygapophysis is moderately tilted upward, and the left one is missing. The synapophyses are eroded, but were massive. It cannot be determined if they were undivided.

Discussion. ─ LSUMG V-21191 has the short centrum and neural spine, zygosphene that is wider than the cotyle, short and indistinct interzygapophyseal ridge, low and wide neural arch, and lack of prezygapophyseal accessory processes that is indicative of *Calamagras* (Holman, 2000). It compares well with *Calamgras weigeli* (SMPSMU 63684) from the middle Miocene of east Texas except the Louisiana specimen has a lower, thinner neural spine.

Genus *Ogmophis*

?*Ogmophis miocompactus* Holman, 1976d

Figures 2-35, 2-36, and 2-37

Referred material. ─ V-21158, 21165, 21232, 21291, four trunk vertebrae from the Stonehenge site; LSUMG V-21292, one anterior trunk vertebra from the Stonehenge site; LSUMG V-21189, 21192, one fragmentary posterior trunk vertebra and one vertebral centrum from the TVOR site.

Description. ─ These vertebrae are worn and fragmentary. They have prominent, wide hemal keels, wide overall vertebral shape, and in posterior view, slightly vaulted neural arches. It is difficult to ascertain because of the degree of wear, but the synapophyses of the Louisiana specimens appear to be undivided into diapophyseal and parapophyseal regions. The subcentral ridges are arched upward.

Discussion. ─ The earliest record of *Ogmophis miocompactus* is from the late Arikareean Mouth of McCann's Canyon Site in Cherry County, Nebraska, while *Ogmophis* cf. *Ogmophis miocompactus* has been recovered from the late Arikareean Armstrong Ranch Quarry in Sioux County, Nebraska, and late Arikareean Split Rock Formation in Fremont County, Wyoming (Figure 2-35; Holman, 1976b, 1979, 1977d, 1981a, 2000). Hemingfordian records of this taxon are limited to the early Hemingfordian Black Bear II Quarry in Bennett County, South Dakota (Figure 2-36; Holman, 1976d, 1979, 2000). Finally, *Ogmophis miocompactus* or *Ogmophis* cf. *Ogmophis miocompactus* are found in three Barstovian localities: The early Barstovian Trinity River Locality in San Jacinto County, Texas (Figure 2-37; Holman, 1977a, 1996, 1979, 2000), the late Barstovian Bijou Hills Locality in Charles Mix County, South Dakota (Figure 2-37; Holman, 1978, 1979, 2000), and the late Barstovian Fort Polk Locality in Vernon Parish, Louisiana (Figure 2-37).

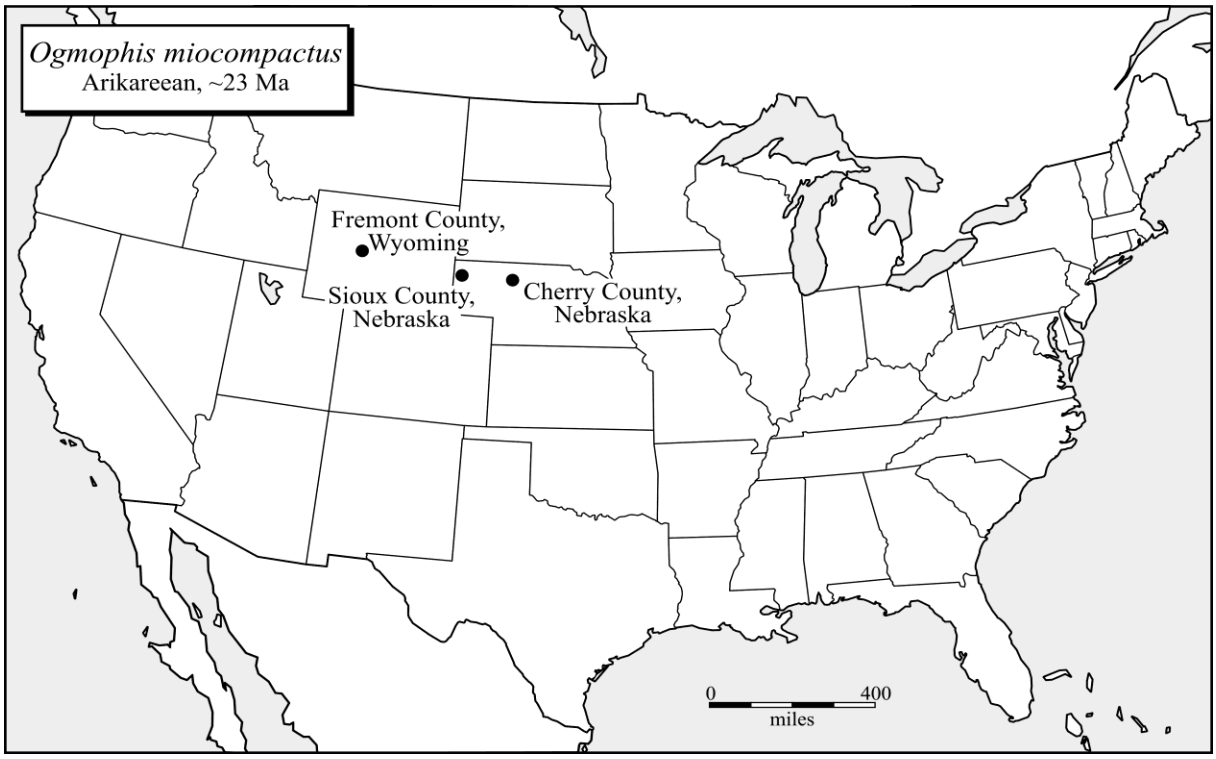

Figure 2-35. North American distribution of Arikareean *Ogmophis miocompactus*.

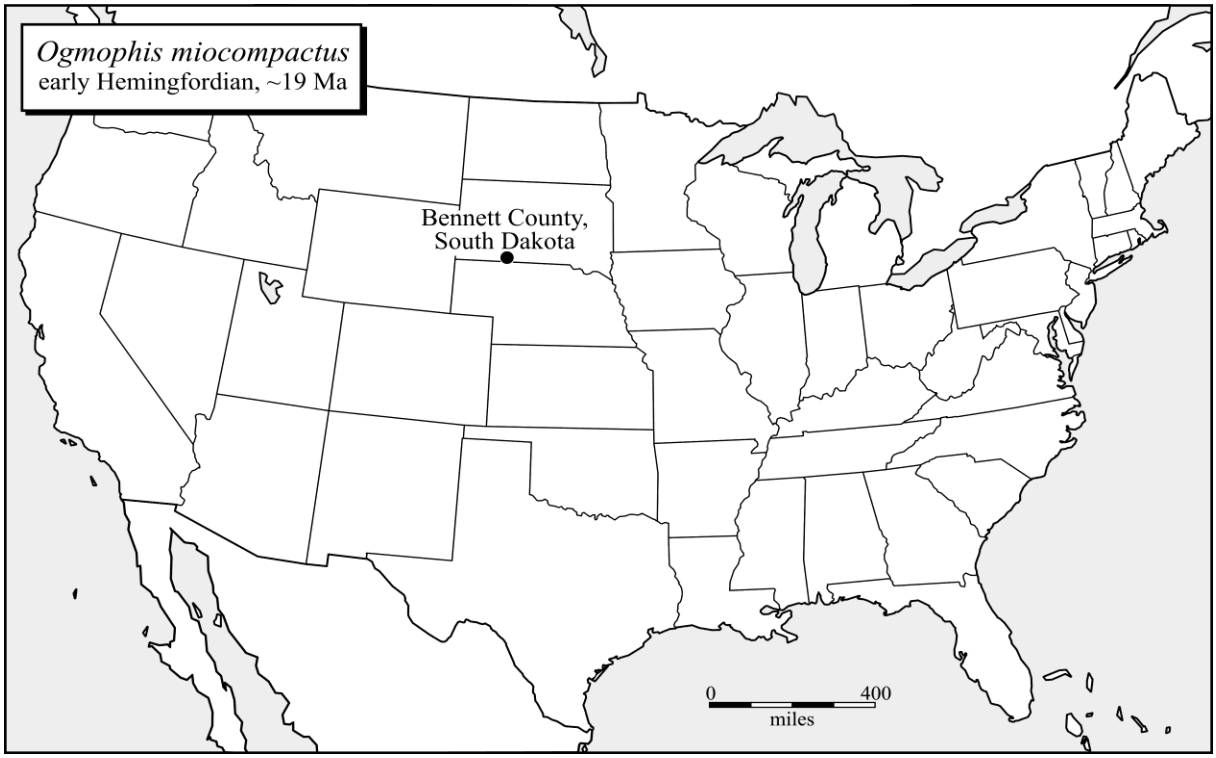

Figure 2-36. North American distribution of Hemingfordian *Ogmophis miocompactus*.

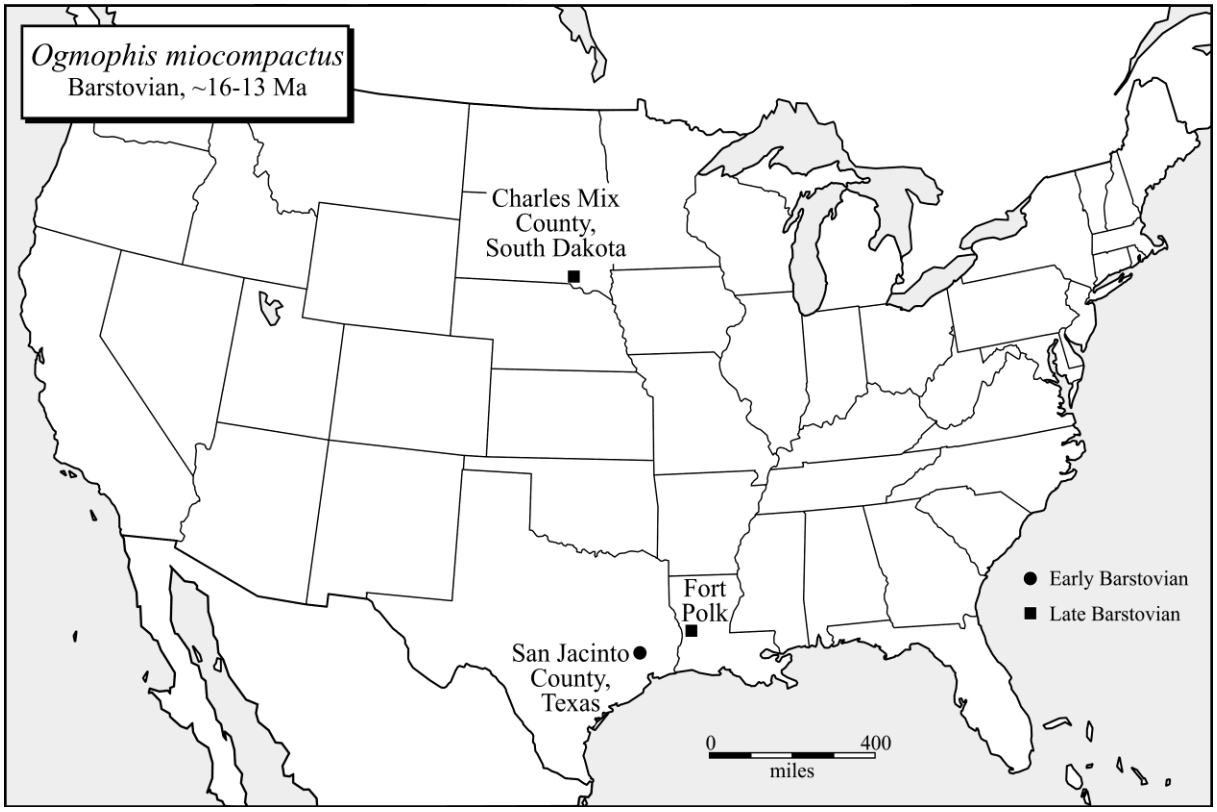

Figure 2-37. North American distribution of Barstovian *Ogmophis miocompactus.*

The preserved portions of these vertebrae compare well with *Ogmophis miocompactus* (SMPSMU 63685) from the Middle Miocene of east Texas. The uniform width of the hemal keel, dorsally-bowed subcentral ridges, and neural spine thickness are similar between the Texas and Louisiana specimens. The Louisiana specimens are not as well-preserved, having only the centrum and hemal keel preserved, and thus are only tentatively regarded as ?*Ogmophis miocompactus*.

It has been suggested that *Ogmophis compactus* and *O. miocompactus* form a clade from the Late Eocene to the Late Miocene that trends toward smaller size, longer and thinner neural spines, anterior thinning of the hemal keel, greater division of the synapophyses, and lateral movement of the prezygapophyseal accessory processes (Rogers, 1976; Parmley, 1984; Holman, 2000). The smaller size and anteriorly thinning hemal keel of the Louisiana specimens is in accordance with the proposed lineage.

Subfamily Erycinae Bonaparte, 1831

Genus and Species indeterminate

Referred material. ─ LSUMG V-3994, one snake (cloacal?) vertebra from the Stonehenge site.

Description. ─ This small snake vertebra is wider than long, which gives it a very robust appearance. From the dorsal view, the neural spine is of medium thickness and extends from the zygantrum to the first third of the prezygapophyseal articular facet. The right prezygapophyseal articular facet is missing; the left one is subrounded and has a short accessory process. The diapophyses extend laterally to the lateral extent of the prezygapophyseal articular facet. From the ventral view, it lacks a ventrally projecting hypapophysis; instead displaying a hemal keel

that is fairly wide and distinct. The centrum is wide and triangular-shaped. Posteriorly, the neural canal is rounded, and the neural arch is moderately depressed. The condyle is worn. The postzygapophyseal articular facets are oval in shape. There are shallow subcentral grooves.

Discussion. ─ Schiebout and Ting (2001) figured this specimen as belonging to the colubrinae; however, the depressed neural arch, lack of paracotylar foramina, and wide vertebral form ally this specimen with the Erycinae. The laterally projecting diapophyses are a conundrum, as this combination of features has not been reported in the literature, and is not seen in the snakes studied thus far. At first glance, it is tempting to call this vertebra a cloacal vertebra, in which the lymphapophyses are not preserved, but it is difficult, if not impossible, to ascertain what might have been in place where processes are broken.

Family Boidae Gray, 1825

Subfamily, Genus and Species indeterminate

Referred material. ─ LSUMG V-21293, 21294, 21295, 21296, four fragmentary trunk vertebrae from the Stonehenge site.

Description/ Discussion. ─ These vertebrae are characterized by large condyles and wide hemal keels. Unfortunately, with the exception of LSUMG V-21293, which has remnants of the neural arch, these vertebrae consist of only a centrum, and thus, cannot be assigned any further than boid.

Family Colubridae Oppel, 1811

Subfamily Colubrinae Cope, 1895

Genus *Ameiseophis* Holman 1976b

Ameiseophis sp.

Figures 2-38, 2-39, and 2-40

Referred material. ─ LSUMG V-4478, 13280, 13221, 13164, four trunk vertebrae from the Stonehenge site.

Description. ─ These are small colubrine vertebrae that are characterized by very prominent hemal keels, subcentral ridges and subcentral grooves. They have rounded condyles, and the cotyles are subrounded in shape. LSUMG V-13164 is more elongate than the other vertebrae. In anterior view, paracotylar depressions are present, as are single paracotylar foramina. The prezygapophyses are moderately tilted upward. In lateral view, the centrum has pronounced fossae posterior and dorsal to the synapophyses containing large foramina, and there are prominent interzygapophyseal ridges. The subcentral ridges are prominent and bowed dorsally. The neural arch is highly vaulted in posterior view (less so in LSUMG V-13280). With the exception of LSUMG V-13164, which has a complete neural spine, the neural spines and zygosphenes are incomplete. The neural spines are thin, with LSUMG V-13280 being slightly thinner than the others. Where preserved, the prezygapophyseal articular facets are oval in outline, and although worn, there appears to have been prezygapophyseal accessory processes. LSUMG V-13164 has a lower neural spine than the other vertebrae.

Discussion. ─ The widespread taxon, *Ameiseophis robinsoni*, first appeared in the late Arikareean lower units of the Split Rock Formation in Fremont County, Wyoming (Figure 2-38; Holman, 1976b, 1979, 2000). *Ameiseophis robinsoni* was also described from the upper units of the Split Rock Formation which ranges in age from the middle Hemingfordian to the late Barstovian (Holman 1976b and 2000), but is considered to be Hemingfordian here because of the strong presence of archaic colubrid snakes (Figure 2-39). Additionally, the only other

Hemingfordian record is from the Pollack Farm Locality in Kent County, Delaware (Figure 2-39; Holman, 1998, 2000). *Ameiseophis* cf. *Ameiseophis robinsoni* was reported from the middle Barstovian Egelhoff locality in Keya Paha County, Nebraska and from the Norden Bridge locality in Brown County, Nebraska (Figure 2-40; Holman, 1976, 1979, 1987, 2000). Late Barstovian records occur from the West Valentine Quarry, Cherry County, Nebraska; the Bijou Hills Locality in Charles Mix County, South Dakota; and Fort Polk inVernon Parish, Louisiana (Figure 2-40; Holman and Corner, unpublished-found in Holman, 2000; Holman, 1978, 1979, 2000).

The extremely prominent hemal keel, subcentral ridges, and subcentral grooves of these vertebrae are the most distinctive features of these vertebrae. These features are so prominent that the slight possibility of them being the remnants of a perfectly worn hypapophysis has been considered; however, the presence of four vertebrae with identically worn hypapophyses makes this improbable.

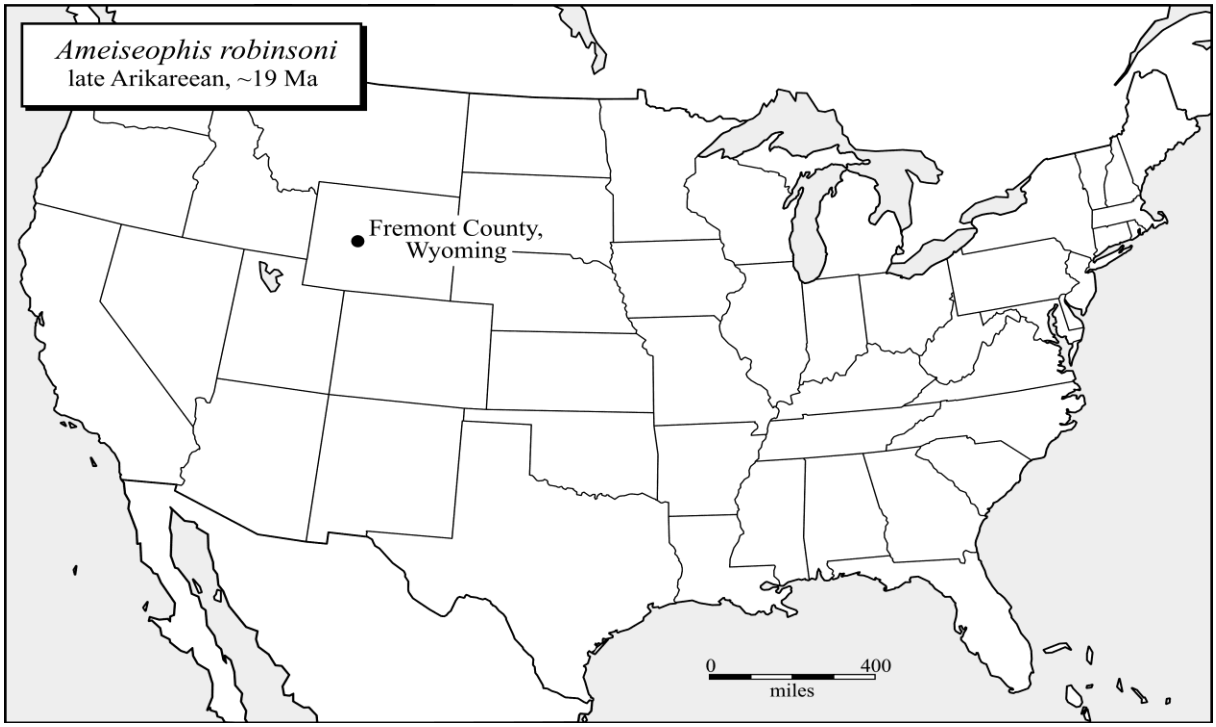

Figure 2-38. North American distribution of late Arikareean *Ameiseophis robinsoni*.

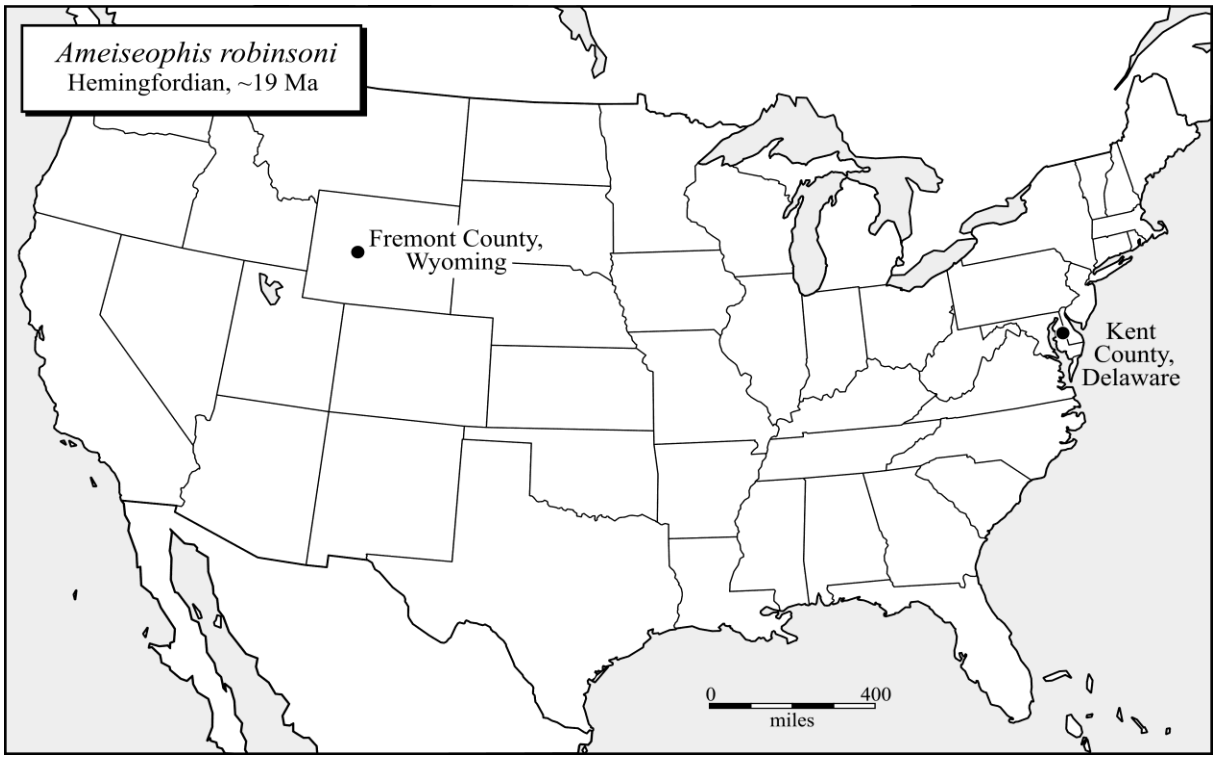

Figure 2-39. North American distribution of Hemingfordian *Ameiseophis robinsoni*.

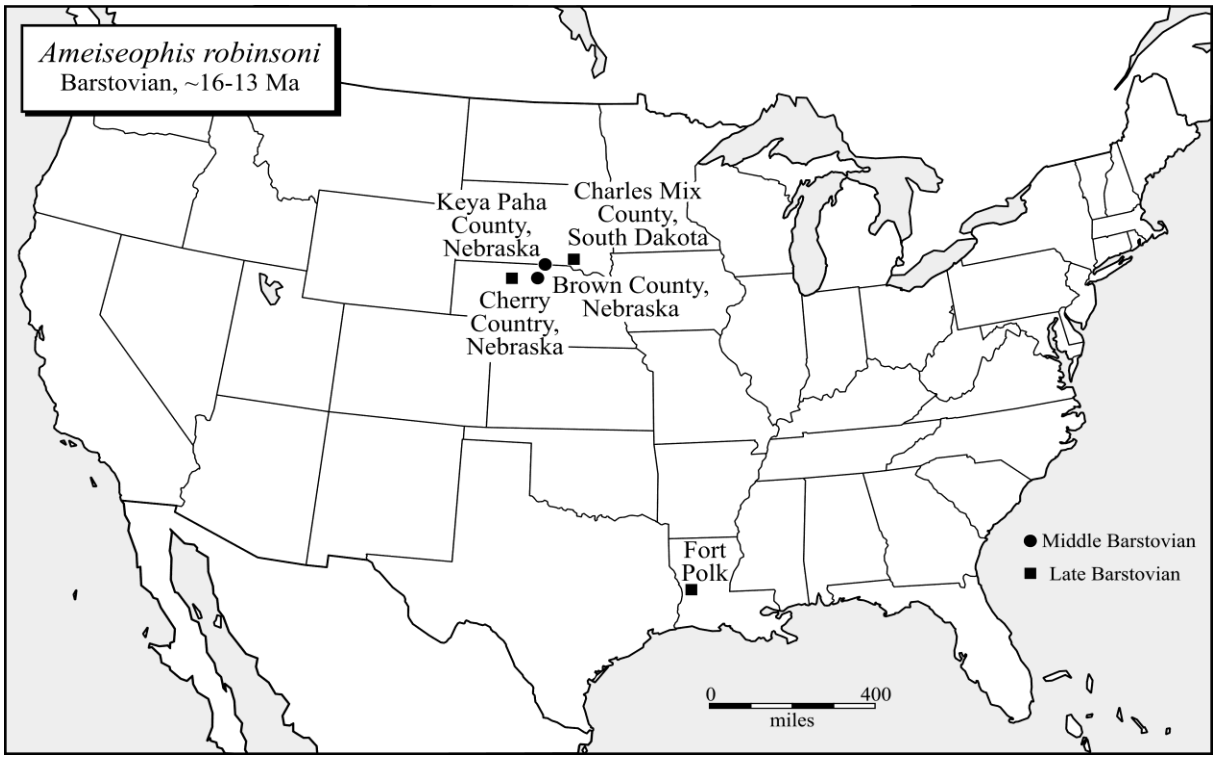

Figure 2-40. North American distribution of Barstovian *Ameiseophis robinsoni*.

The extreme development of the hemal keel coupled with deep subcentral grooves ally these vertebrae to the monotypic genus *Ameiseophis*.

Genus *Salvadora*

Salvadora cf. *Salvadora paleolineata*.

Figure 2-41, 2-42, 2-43, 2-44

Referred material. ─ LSUMG V-21131 and 21132, two trunk vertebrae from the Stonehenge site; LSUMG V-21134, one trunk vertebra from the TVOR site; LSUMG V-21133, one trunk vertebra from the TVOR SE site;

Description. ─ Viewed dorsally the neural spine of LSUMG V-21133 is prominent, slightly worn, and extends from the zygantrum (overhanging it slightly) to just posterior of the eroded zygosphene. The left prezygapophyseal articular facet is missing; the right one is eroded. From the lateral view, the subcentral ridges are weakly developed and the prominent hemal keel is visible. The interzygapophyseal ridges bow dorsally, and there are large lateral foramina just ventral to them. The synapophyses are eroded. Viewed ventrally there is a prominent hemal keel that indistinctly blends into the cotyle and terminates before the lip of the condyle. This posterior terminus broadens to become spatulate-shaped. Subcentral grooves are indistinct, and there is one foramen flanking each side of the hemal keel. The right postzygapophyseal articular facet is broken, such that the original shape cannot be determined; whereas the left postzygapophyseal articular facet appears reniform in shape. Posteriorly, the condyle is rounded and about the size of the neural canal. The anterior cotyle is round, except the ventral portion which is flattened. There are prominent paracotylar foramina: one to the left and one large and two small to the right of the cotyle. Viewed anteriorly, the neural canal is slightly convex ventrally, with the lateral

walls slightly tapering and constricting slightly about midway up the dorsal border of the canal, which is convex dorsally. The neural arch is slightly to moderately vaulted.

LSUMG V-21134 is a well-preserved vertebra that has a long, moderately thin neural spine, extending from the zygantrum, which it slightly overhangs, to slightly posterior to the zygosphene border. The zygosphene margin is broken. The left prezygapophysis is missing; the right prezygapophyseal articular facet is subtriangular in shape. Laterally, the hemal keel is well-developed, and does not extend beyond the condyle. The subcentral ridges are anteriorly bowed upward. There is a prominent foramen ventral to the interzygapophyseal ridges. The ridges are not bowed upward. The synapophyses are eroded but appear to have been prominent and had parapophyseal and diapophyseal portions that were connected. In ventral view, the posterior point of the hypapophysis does not extend beyond the condylar lip. The middle portion of the hemal keel is worn or broken. Subcentral grooves were extremely shallow, if present at all. The right postzygapophyseal articular facet is a rounded diamond shape; the left one has eroded margins. No foramina flank the hemal keel. Viewed from the posterior, the condyle is round and slightly smaller than the neural canal. The postzygapophyseal articular facets are angled slightly upward. From the anterior, the cotyle is round, except for the ventral margin, which is flat. There are moderately deep paracotylar depressions adjacent to the cotyle, each containing a foramen. The prezygapophyseal articular facets are slightly angled upward and the anterior edge of the zygosphene is broken but thickened. The neural arch is slightly vaulted.

LSUMG V-21131 and 21132 are medium-sized colubrine trunk vertebrae thar are nearly complete except for the slightly eroded synapophyses and broken left prezygapophysis on LSUMG V-21132. From the dorsal view, the overall shape is about as wide as long. The neural spine is thin and prominent, extending from the zygantrum to slightly posterior of the

zygosphene. The zygosphene of LSUMG V-21131 is complete and is convex in the middle; whereas the zygosphene of LSUMG V-21132 is straight from the dorsal view. The prezygapophyseal articular facets are ovoid in shape and slightly worn on the edges. Slightly worn prezygapophyseal accessory processes extend anterolaterally from the prezygapophyseal articular facets. Viewed laterally, the neural spine slightly overhangs the zygantrum, and is slightly longer than tall. The interzygapophyseal ridges bow very slightly dorsally and there is a nutrient foramen just ventral to them. The synapophyses are slightly eroded, but the distinct diapophyseal and parapophyseal portions can be discerned. The prominent subcentral ridges are moderately bowed upward, and there are distinct subcentral grooves between them and the prominent hemal keel. Ventrally, the hemal keel is moderately thick, extends from the cotylar lip where it flairs out, is slightly constricted in the middle, and flairs posteriorly, where it contacts the slightly worn condyle. Subcentral paramedian lymphatic fossae and processes on the ventrolateral surface cotylar edge are present on LSUMG V-21131. The postzygapophyseal articular facets are ovoid to subrounded. In posterior view, the slightly worn condyle is round and slightly smaller than the neural canal. The postzygapophyseal articular facets are angled slightly upward. The neural arch is moderately vaulted. Anteriorly, the edge of the zygosphene is moderately thickened. The prezygapophyseal articular facets are slightly tilted upward. The cotyle is round, except for the flattened ventral portion, and there is a deep paracotylar fossa on each side of the cotyle, containing a large paracotylar foramen.

Discussion. ─ The evolutionary history of the ubiquitous *Salvadora paleolineata* begins in the early Hemingfordian Black Bear Quarry II in the Rosebud Formation of South Dakota (Figure 2-41; Holman1976d, 1979, 2000), and the Marsland Quarry, Marsland Formation, South Dakota (Figure 2-41; Holman, 1977d, 1979, 2000). The taxon is known from the early Barstovian

Trinity River and Town Bluff localities in eastern Texas (Figure 2-42; Holman, 1977, 1979, 1996, 2000) and the Split Rock Formation, Upper Units of Wyoming (Figure 2-42; Holman, 1976, 1979, 2000). Middle Barstovian records are known from the Egelhoff locality, Brown County, Nebraska (Figure 2-42; Holman, 1973a, 1979, 1987, 2000), the Hottel Ranch Rhino Quarries, Banner County, Nebraska (Figure 2-42; Holman, 2000), and the Norden Bridge Locality, Brown County, Nebraska (Figure 2-42; Holman, 1973b, 1979, 2000). Late Barstovian *Salvadora paleolineata* records are numerous and include the Nebraska localities, Annies Geese Cross locality, Knox County (Figure 2-42; Holman, 2000), Glad Tidings Quarry, Knox County (Figure 2-42; Holman, 1996b, 2000), Myers Farm site, Webster County, Nebraska (Figure 2-42; Holman, 1977b, 1979, 2000), Railway Quarry B, Cherry County (Figure 2-42; Holman and Sullivan, 1981; Holman, 2000), West Valentine Quarry, Cherry County (Figure 2-42; Holman and Corner, unpublished-found in Holman, 2000). Other late Barstovian localities include the Bijou Hills locality in Charles Mix County, South Dakota (Figure 2-42; Holman, 1978, 1979, 2000), and Fort Polk in Vernon Parish, Louisiana (Figure 2-42). Middle Hemphillian records include the Lemoyne Quarry in Keith County, Nebraska (Figure 2-43; Parmley and Holman, 1995; Holman, 2000), and the Coffee Ranch locality in Hemphill County, Texas (Figure 2-43; Parmley, 1984; Holman, 2000).

The most striking aspect of these vertebrae is the nice preservation from Fort Polk. Additionally, the subcentral paramedian lymphatic fossae of LSUMG V-21131 are very evident in ventral view. LaDuke (1991) states that this under-discussed feature is found primarily in posterior trunk vertebrae, and that they contain the "segmental dilations of the longitudinal paravertebral internal lymphatic vessels."

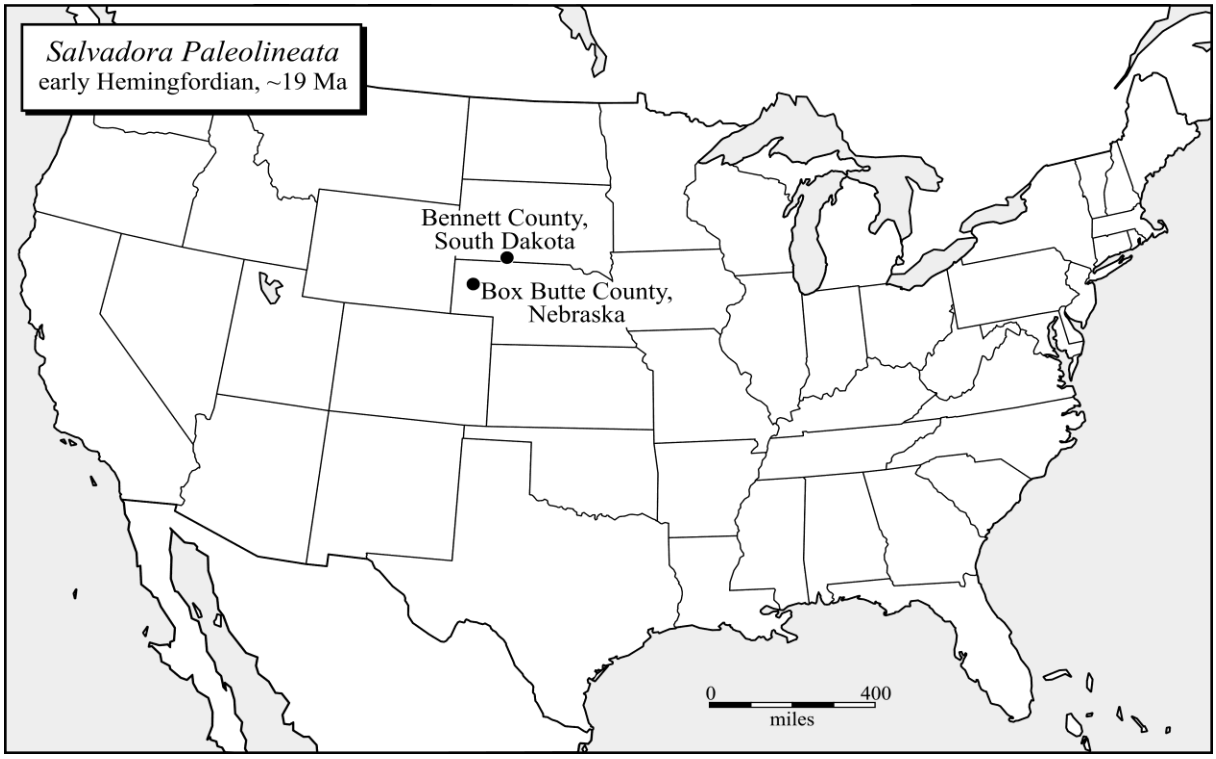

Figure 2-41. North American distribution of early Hemingfordian *Salvadora paleolineata*.

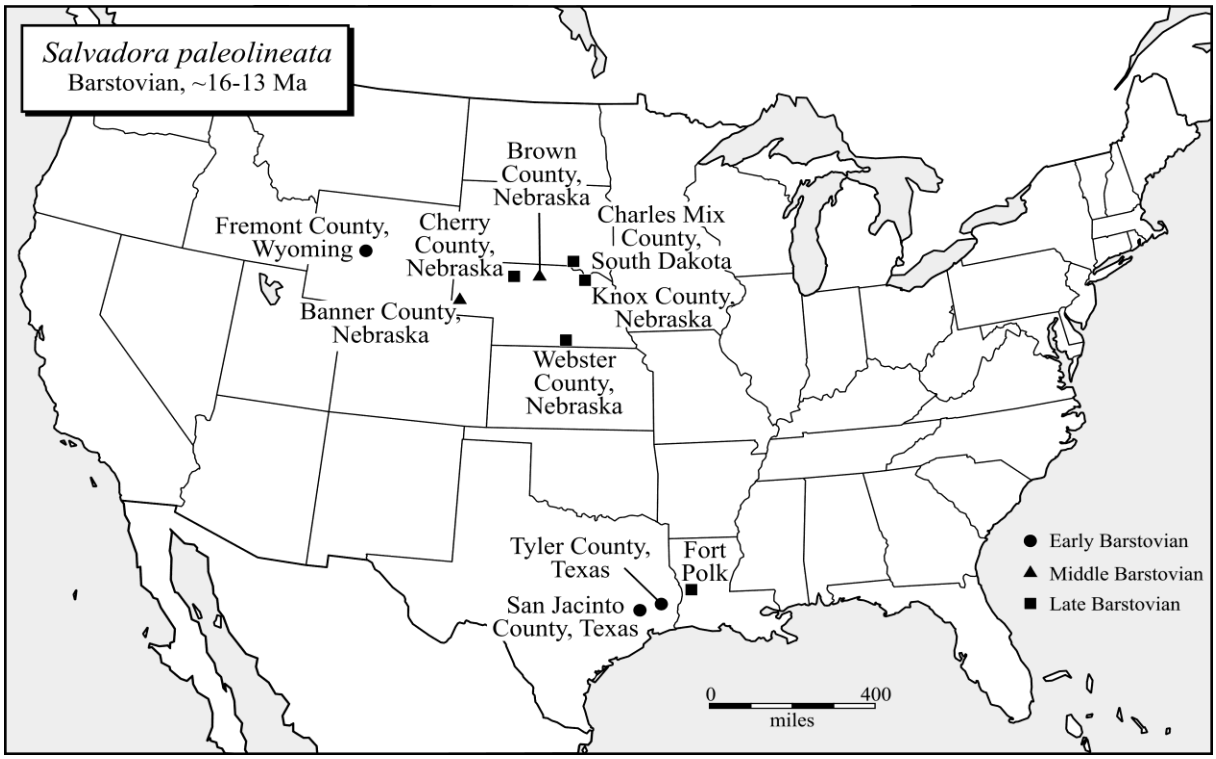

Figure 2-42. North American distribution of Barstovian *Salvadora paleolineata*.

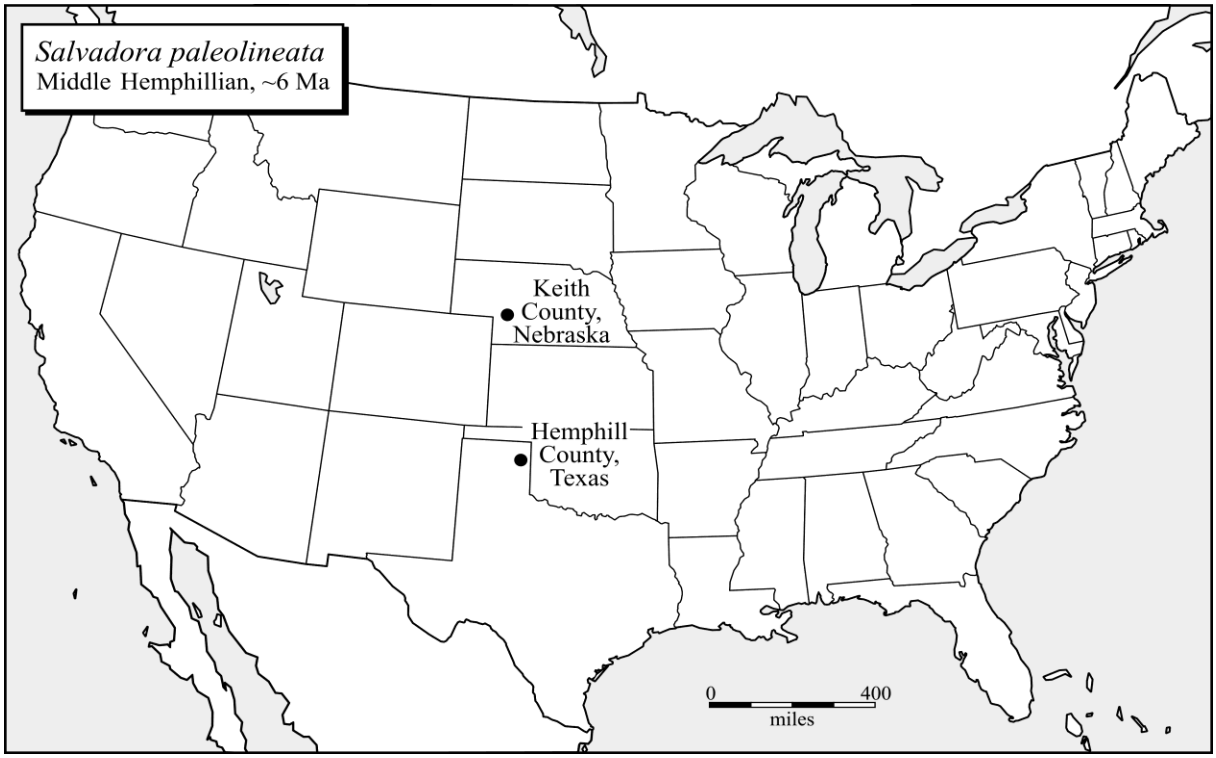

Figure 2-43. North American distribution of middle Hemphillian *Salvadora paleolineata*.

Furthermore, the presence of minute processes on the ventrolateral aspect of the cotylar lip and a slight dorsally upward curve of the hemal keel just posterior to the cotyle suggest a posterior trunk vertebra (LaDuke, 1991). The ventrolateral processes of the cotyle are an attachment point for a ligament that extends from the capitulum of the rib, and the slight notch in the hemal keel just posterior to the cotyle "allows passage of the transverse anastamosing tracts of the longitudinal paravertebral internal lymphatic vessel" (LaDuke, 1991). The presence of these features on LSUMG V-21131 makes it a posterior trunk vertebra.

Comparisons with Miocene *Elaphe nebraskensis* (synomized with *Elaphe kansensis* by Holman (2000)) at the University of Nebraska State Museum (UNSM 46505) and the Shuler Museum of Paleontology Southern Methodist University (SMPSMU 63689) show that *Elaphe*

kansensis vertebrae are much wider than long (more robust overall), have more distinct subcentral grooves, and a hemal keel that begins at the cotylar lip.

Miocene *Dakotaophis greeni* from Trinity River (SMPSMU 63686) have thinner neural spines and much smaller postzygapophyseal articular facets that are more oval-shaped than LSUMG V-21133. The hemal keels are similar between the Fort Polk and Trinity River specimens, in that they constrict midway along the length and flare posteriorly, giving a spatulate terminus.

Compared to *S. paleolineata* (UNSM 46500) from Myers Farm, Nebraska, LSUMG V-21133 has a cotyle similar in shape, but this appears to be a variable character in the Nebraska specimens. In addition, the neural spine of LSUMG V-21133 is thicker and slightly longer than most of the Nebraska Myers Farm specimens examined. The subcentral ridges are bowed dorsally, but this character was not present on all Nebraska specimens examined.

LSUMG V-21133 and 21134 are closely comparable to the genus *Salvadora.* Compared to *Salvadora paleolineata* from the Trinity River site in east Texas SMPSMU 63687, the hemal keel of LSUMG V-21133 does not extend ventrally from the centrum as much as the Texas specimens; whereas, LSUMG V-21134 does. Furthermore LSUMG V-21133 has a slight constriction about midway along its length, and has a spatulate posterior terminus not seen in the Texas specimens. LSUMG V-21134 has the more uniformly thin hemal keel of *Salvadora paleolineata.* The Louisiana specimens share with *S. paleolineata* zygapophyseal articular facets that have a large surface area. Although eroded, the synapophyses of the Louisiana specimens are more robust than the four Texas specimens examined. Additionally, Holman (1973) states "the zygosphene is convex dorsally" in the holotype (UMMP No. V56292), and this character is present in the Louisiana specimens; however, this character is not found in all of the four

specimens from eastern Texas. The largest vertebra of the four (similar in size to LSUMG V-21133 and 21134) does not display this character; instead, the zygosphene is flattened dorsally when viewed from the anterior

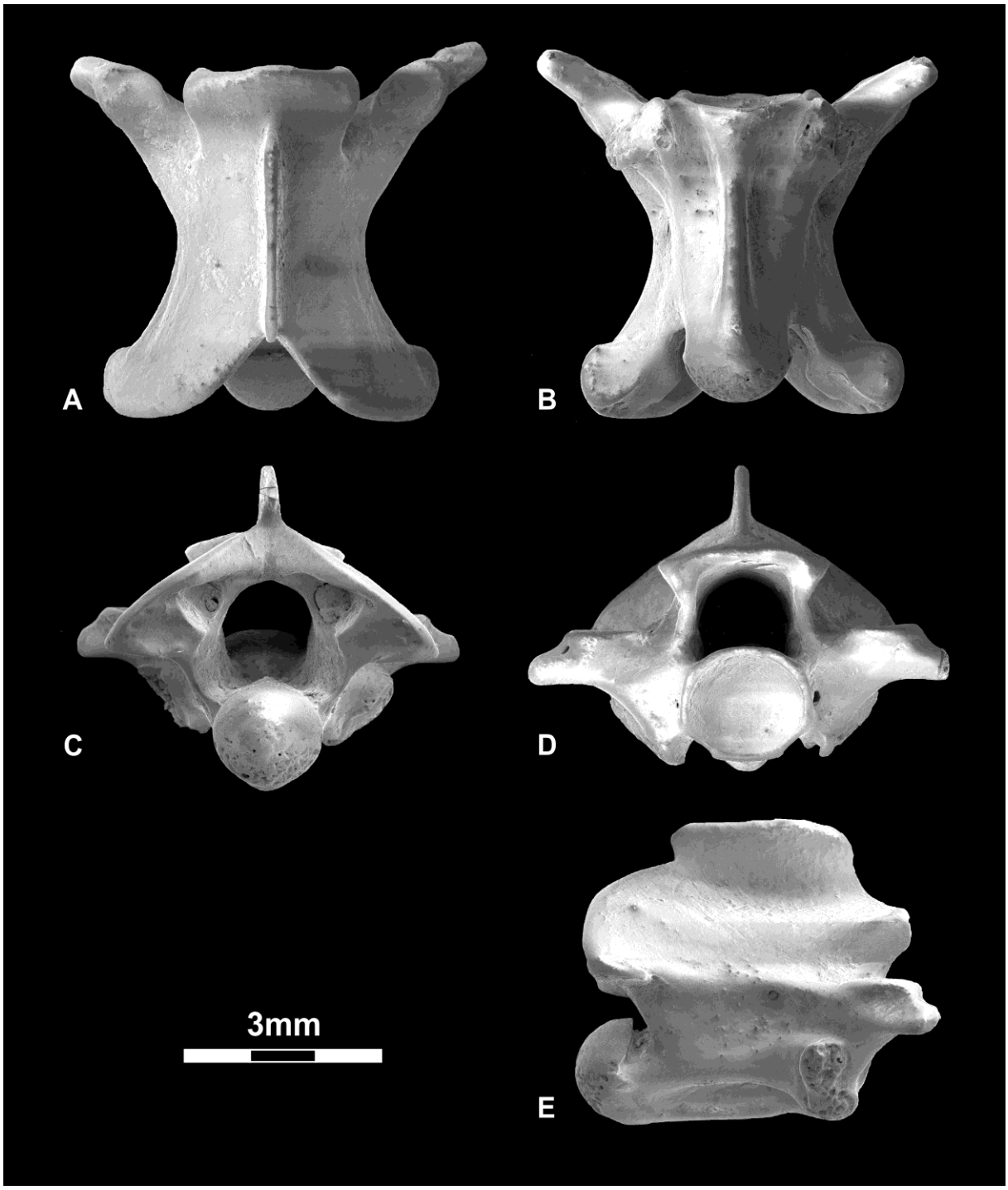

Figure 2-44. Scanning electron micrographs of *Salvadora* sp. (LSUMG V-21133) trunk vertebra in A. dorsal view; B. ventral view; C. posterior view; D. anterior view; and E. right lateral view.

Genus *Nebraskophis*

Nebraskophis cf. *Nebraskophis skinneri*

Figures 2-45 and 2-46

Referred material. ─ LSUMG V-21208, 21209, two posterior trunk vertebrae from the Stonehenge site.

Description. ─ LSUMG V-21208 is well-preserved with an elongate vertebral form. Dorsally, the neural spine extends from the zygantrum well onto the convex zygosphene. The right prezygapophyseal articular facet is an elongated oval shape. Laterally, the neural spine is long and low, well over two times as long as high, and slightly overhangs the zygantrum. The interzygapophyseal ridge is very well-developed, as are the synapophyses, which are too eroded to determine if they are divided or not. The subcentral ridges are bowed upward, and the subcentral grooves are shallow. The condyle is oblique. The hemal keel is fairly prominent and flat, except for a slight dorsal bow anteriorly. Ventrally, the hemal keel is rounded anteriorly where it is bowed dorsally, and then becomes wider and flatter beginning at about of one third of its length posterior to the cotyle. Subcentral paramedian lymphatic fossae are present between the lateral edge of the cotyle and the synapophyses. Anteriorly, the cotyle is subrounded and is flanked by paracotylar fossae, each containing one foramen. The prezygapophyseal articular facet is flat or angled very slightly downward. The zygosphene is bowed dorsally and is not dorsoventrally thickened. Posteriorly, the neural arch is moderately vaulted, and the condyle is round.

LSUMG V-21209 is more fragmentary than LSUMG V-21208, but shares the elongate vertebral morphology, long and low neural spine, well-developed interzygapophyseal ridges and flat hemal keel in lateral view. The hemal keel does not, however, have the rounded area

anteriorly that LSUMG V-21208 has. Furthermore, the interzygapophyseal ridges, though prominent, are not as defined as LSUMG V-21208.

Discussion. ─ The earliest occurrence of *Nebraskophis skinneri* is from the middle Barstovian Egelhoff and Norden Bridge localities in Nebraska (Figure 2-45; Holman, 1973a, 1976, 1979, 1987, 2000). Late Barstovian records are found at the Myers Farm Site in Webster County, Nebraska (Figure 2-45; Holman, 1977b, 1979, 2000), and the Fort Polk locality, while middle Hemphillian *Nebraskophis skinneri* are found at the Lemoyne Quarry, Keith County, Nebraska (Figure 2-46; Parmley and Holman, 1995; Holman, 2000).

The most striking aspects of these vertebrae are the elongated vertebral form and unique hemal keel morphology of LSUMG V-21208. *Texasophis fossilis* and *Dakotaophis skinneri* are two Miocene colubrines with an elongate vertebral form (Holman, 2000). Compared to the holotype *Texasophis fossilis* (SMPSMU 63691) from the early Barstovian Town Bluff site in eastern Texas, the Louisiana specimens are more elongate; have longer, thinner neural spines; hemal keels that are not as well-developed and extend more posteriorly; and deeper subcentral grooves.

The interzygapophyseal ridges are similar in their degree of development. LSUMG V-21208 and 21209 share the elongate vertebral form, long and low neural spine, well-developed interzygapophyseal ridges, fairly prominent hemal keel that is moderately narrow, and oval prezygapophyseal articular facets with *Nebraskophis skinneri*. Differences between the taxa include the unique hemal keel shape of LSUMG V-21208 and that the neural spine slightly overhangs the zygantrum; whereas *Nebraskophis skinneri* has its "posterior end sloping gently into the neural arch" (Holman, 2000). Given these differences, LSUMG V-21208 and 21209 cannot be assigned to the specific level.

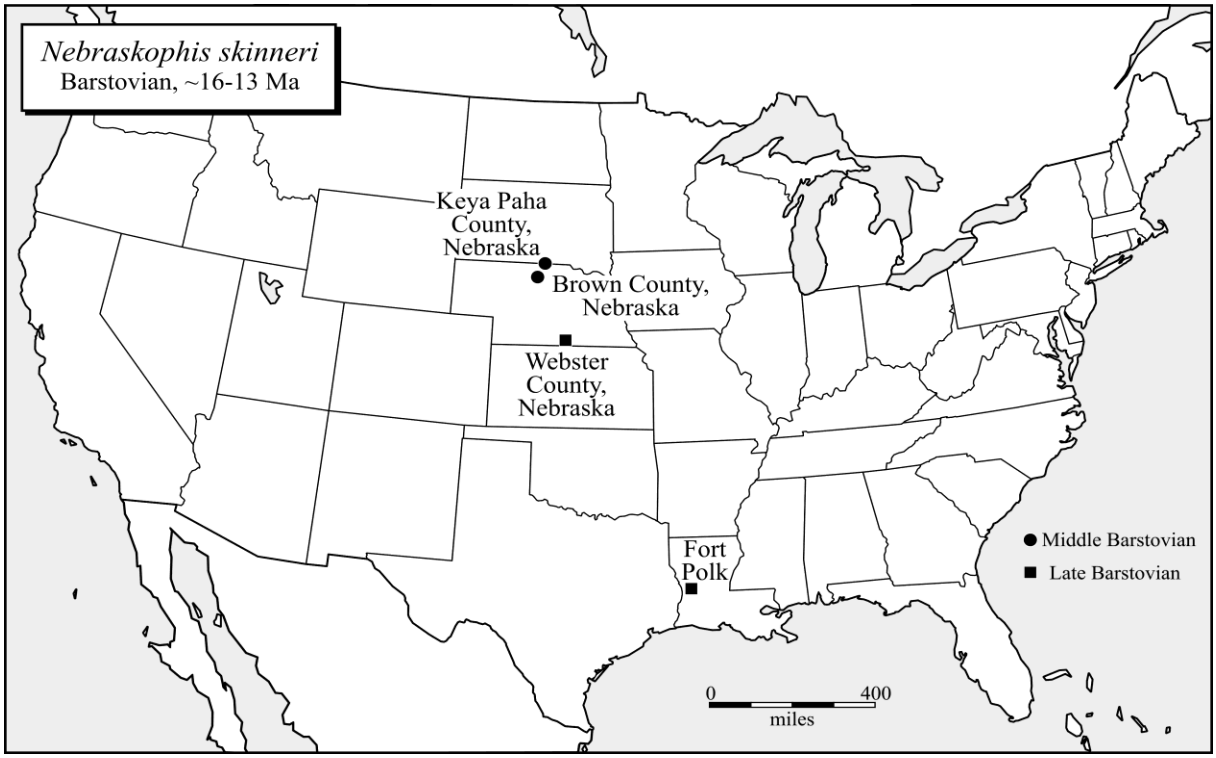

Figure 2-45. North American distribution of Barstovian *Nebraskophis skinneri*.

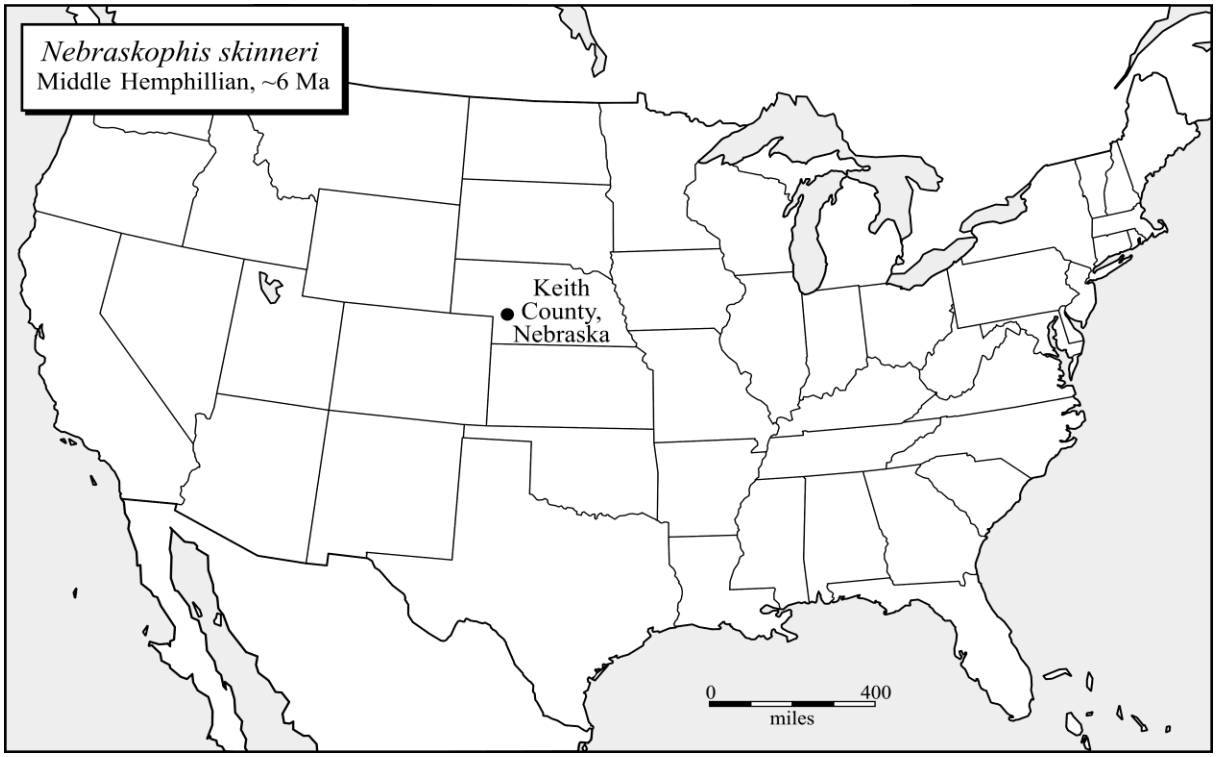

Figure 2-46. North American distribution of middle Hemphillian *Nebraskophis skinneri*.

Subfamily Colubrinae Cope, 1895

Genus and Species indeterminate

Referred material. ─ LSUMG V-13216, 21176, two fragmentary trunk vertebrae from the Stonehenge site.

Description. ─ These vertebrae are medium- to large-sized colubrine trunk vertebrae. Viewed dorsally, the neural arch of LSUMG V-13216 has the remnants of a thick neural spine and zygosphene. The left prezygapophyseal articular facet is oval in shape; the right prezygapophyseal articular facet is missing. Viewed ventrally, the hemal keel is very prominent and extends from the outer edge of the cotyle to the condyle. It flairs out at the edge of the condyle, does not extend beyond the condylar lip, and is accompanied by fairly deep subcentral grooves and ridges. The postzygapophyseal articular facets are too worn to determine a shape. In lateral view, the subcentral ridges are slightly bowed upward, and the centrum has pronounced fossae posterior and dorsal to the synapophyses containing large foramina. The synapophyses are worn, but were large, and it cannot be determined whether they were undivided or not. In posterior view, the round condyle is approximately the size of the neural canal, and the neural arch is moderately vaulted. Anteriorly, the cotylar margin is eroded, but appears to have been rounded with a flat ventral surface. There is a paracotylar depression flanking the cotyle under the left prezygapophyseal articular facet. The depression contains a small foramen extending under the edge of the cotyle. This same area to the right of the cotyle is eroded. The left prezygapophyseal articular facet is fairly flat, not angled upward. To the left of the cotyle, there is a prominent depression without a visible foramen; the same area to the right of the cotyle is missing. The right postzygapophyseal articular facet is oval-shaped, and the left one is broken.

LSUMG V-21176 shares the same features as LSUMG V-13216 except it is slightly larger with a more vaulted neural arch. Additionally, it has postzygapophyseal articular facets that have a greater lateral extent, visible in dorsal view.

Discussion. ─These medium-sized colubrine vertebrae are robust and slightly wider than they are long. The most striking features are the thick neural spines, prominent hemal keels, and deep fossae containing a small lateral foramen. *Elaphe nebraskensis* (*kansensis*) from the Town Bluff site in eastern Texas (SMPSMU 63689) has a thicker hemal keel that does not flair posteriorly as much as LSUMG V-13216, a thinner neural spine, and less prominent fossae on the lateral surface of the centrum. The hemal keel of the Louisiana specimens are indistinguishable from modern *Lampropeltis getula* examined from the UNSM, but the vertebrae are more robust and have a longer, thicker neural spine. The thickness of the neural spine, coupled with the extremely prominent nature of the hemal keel, is not similar to any known modern or fossil species seen thus far.

Subfamily Colubrinae Cope, 1895

Genus and Species indeterminate

Referred material. ─ LSUMG V-3995, 3996, 21210, 21211, 21212, 21188, 13218, 21228, 21229, 9120, 21230, 21231, 21233, 21234, 21235, 13214, 21240, 21241, 21242, 21243, 21244, 21245, 21246, 21247, 21248, 21249, 21250, 21251, 21252, 21253, 21254, 21255, 21256, 21257, 34 fragmentary vertebrae from the Stonehenge site; LSUMG V-21193, 21194, 21195, 21196, 21197, 21198, six fragmentary centra from the TVOR site; LSUMG V-21223, one vertebra from the TVOR Southeast site; LSUMG V-21214, 21236, two fragmentary vertebra from the TVOR N. Creek site; LSUMG V-21127, one vertebral centrum from the Discovery site.

Description/Discussion. ─ These vertebrae are too fragmentary to identify below the subfamilial level. Many are just represented by a centrum, with important diagnostic features such as neural spines, degree of neural arch vaulting, well-preserved hemal keels, and pre- and postzygapophyses not preserved.

Subfamily Natricinae Bonaparte, 1840

Genus *Neonatrix* Holman, 1973

Neonatrix elongata

Figures 2-47, 2-48, and 2-49

Referred material. ─ LSUMG V-21174, one trunk vertebra from the Stonehenge site.

Description. ─ This small, elongate vertebra has a poorly developed hypapophysis on the ventral part of the centrum. Dorsally the neural spine is almost completely missing, but judging by the broken area, was thin and extended from the zygantrum well onto the zygosphene. The prezygapophyseal articular facets are subrounded to oval in shape, but the margins may not be complete. The left postzygapophyseal articular facet is pentagonal-shaped, and the right one is roughly diamond-shaped.

Discussion. ─ *Neonatrix elongata* first appears in the early Hemingfordian of Bennett County, South Dakota (Figure 2-47; Holman1976d, 1979, 2000), and by the early Barstovian appears in Polk, Tyler, and San Jacinto counties in Texas (Figure 2-48; Holman 1977a, 1979, 1996, 2000). Middle Barstovian records for *Neonatrix elongata* are limited to the Egelhoff locality in Keya Paha County, Nebraska (Holman, 1973a, 1979, 1987, 2000), and the Norden Bridge locality in Brown County, Nebraska (Figure 2-48; Holman, 1973b, 1979, 2000). By the late Barstovian, *Neonatrix elongata* was more widespread having been recovered from the Myers Farm locality

in Webster County, Nebraska (Figure 2-48; Holman, 1977b, 1979, 2000), the Railway Quarry B in Cherry County, Nebraska (Figure 2-48; Holman and Sullivan, 1981; Holman, 2000), the West Valentine Quarry in Cherry County, Nebraska (Figure 2-48; Holman and Corner, unpublished-found in Holman, 2000), the Bijou Hills locality in Charles Mix County, South Dakota (Figure 2-48; Holman, 1978, 1979, 2000), and the Fort Polk locality in Vernon Parish, Louisiana (Figure 2-48). The only Hemphillian record is from the middle Hemphillian Lemoyne Quarry in Keith County, Nebraska (Figure 2-49; Parmley and Holman, 1995; Holman, 2000).

Although a slightly smaller, LSUMG V-21174 is very similar to *Neonatrix elongata* (SMPSMU 63692) from the east Texas, early Miocene Town Bluff site. sharing the elongate vertebral form, long and thin neural spine, and poorly developed posterior projection of the hypapophysis. The only difference between the Texas and Louisisana specimens, is LSUMG V-21174 has a more pronounced hypapophysis anteriorly, where it meets the cotyle.

Genus *Neonatrix* Holman, 1973

Neonatrix sp.

Referred material. ─ LSUMG V-13217, 13219, 12740, 13220, four trunk vertebrae from the Stonehenge site; LSUMG V-21205, 21213, two trunk vertebrae from the TVOR site; LSUMG V-21221, 21222, two trunk vertebrae from the TVOR Southeast site.

Description. ─ LSUMG V-13217 is a small natricine vertebra. Viewed dorsally, the worn neural spine begins at the zygantrum border and does not contact the zygosphene. The broken prezygapophyseal articular facet appears to have been oval-shaped. In lateral view, the ventral portion of the centrum has a worn hypapophysis.

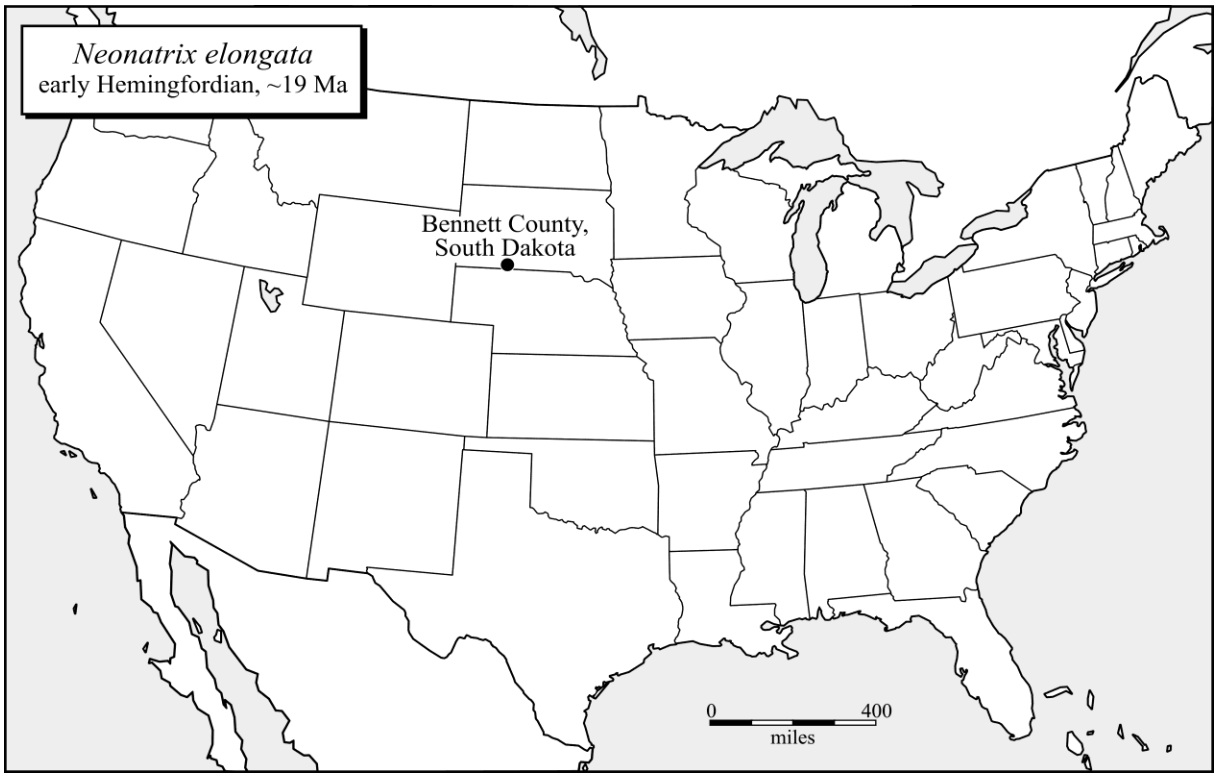

Figure 2-47. North American distribution of Hemingfordian *Neonatrix elongata*.

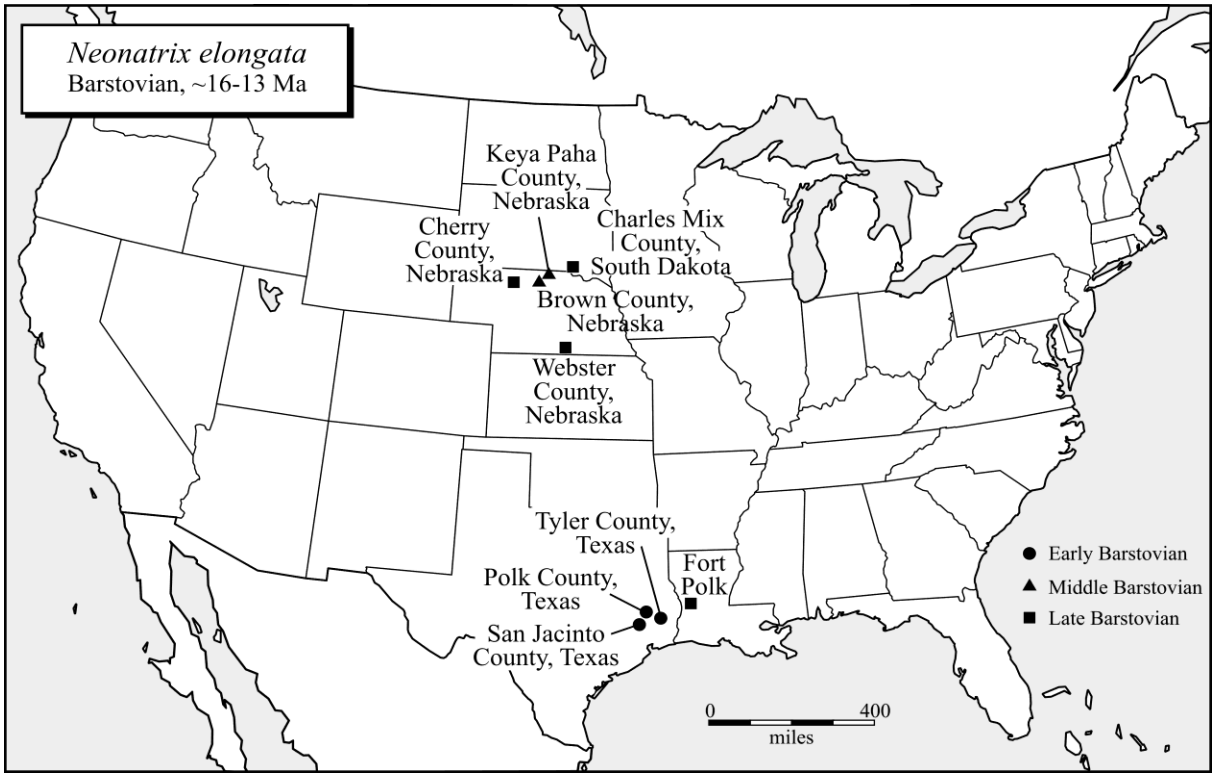

Figure 2-48. North American distribution of Barstovian *Neonatrix elongata*.

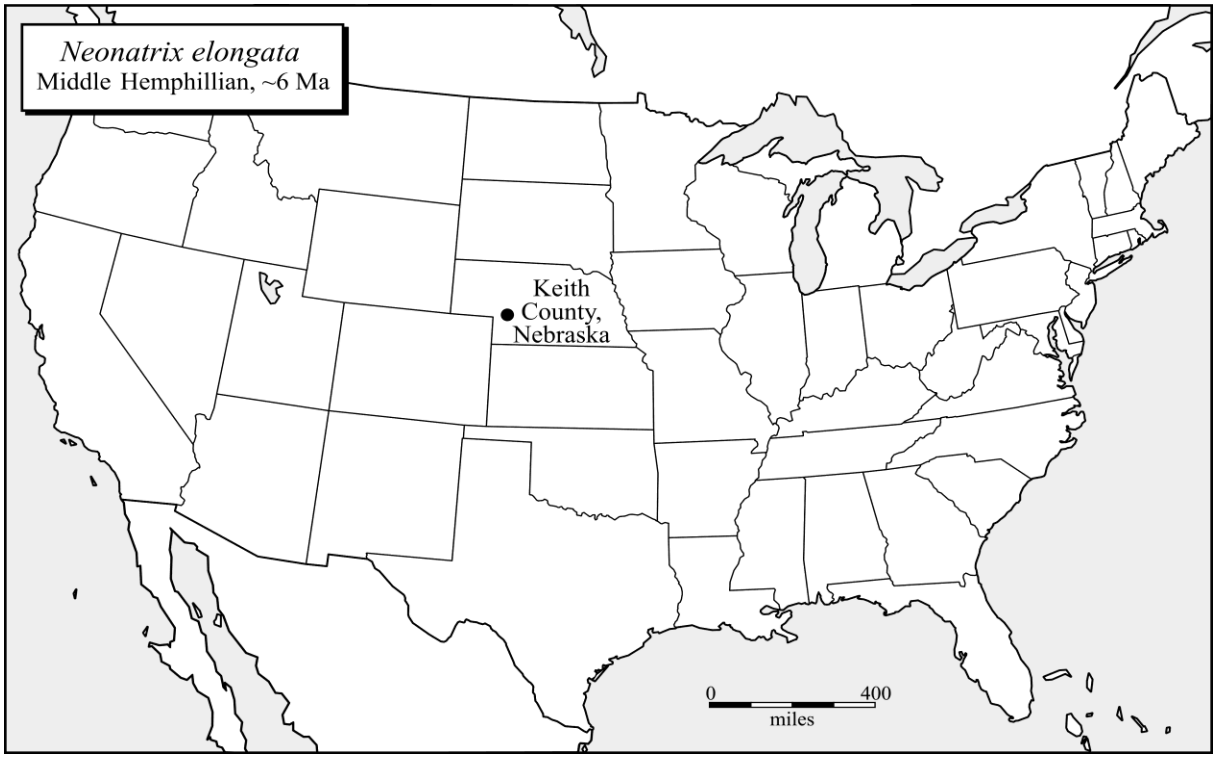

Figure 2-49. North American distribution of middle Hemphillian *Neonatrix elongata*.

Subfamily Natricinae Bonaparte, 1840

LSUMG V-12740 is a small natricine trunk vertebra. The partially broken hypapophysis is less than one-third of the condyle thickness. The condyle and cotyle are round in shape. Deep paracotylar depressions flank either side of the cotyle; no paracotylar foramina are evident. The neural arch is moderately vaulted in posterior view. Because the neural spine is broken, it cannot be determined whether it was longer than high. However, it is a prominent feature and is about as thick as a comparably-sized *Thamnophis* neural spine. The zygosphene is slightly broken but appears moderately convex in dorsal view. The right prezygapophyseal articular facet is sub-rounded; the left one is incomplete. The postzygapophyseal articular facets are oval in outline. Laterally, this vertebra has worn prezygapophyseal accessory processes. The interzygapophyseal ridge is slightly concave. The synapophyses are slightly worn and indistinctly divided into ventral parapophyses and dorsal diapophyses.

Discussion. ─ The presence of a much reduced hypapophysis and thin hemal keel (Holman, 1977, 2000) ally these specimens to the genus *Neonatrix.* The above referred specimens not described share the features referable to *Neonatrix* sp. and differ from *Nerodia* in having a more elongate vertebral form and *Thamnophis* in the reduced hypapophysis (Holman, 1977, 2000).

Natricine Genus and Species Indeterminate

Referred material. ─ LSUMG V-13215, 4479, 10200, 9118, 21259, 21260, 21261, 21262, 21263, 21264, 21275, 21276, 21277, 21286, 14 trunk vertebrae from the Stonehenge site; LSUMG V- 21237, one fragmentary vertebra from the TVOR N. Creek site.

Description. ─ These vertebrae are all variably worn. They all have hypapophyses on the ventral part of the centrum; however, most are broken before their posterior terminus.

Discussion. ─ Because of the fragmentary nature of these vertebrae, identification to the generic or specific level is not possible. They are clearly not colubrine vertebrae based on the presence of hypapophyses. They are excluded from colubrine anterior trunk (cervical) vertebrae, which bear hypapophyses, based on the presence of relatively smaller neural canals and larger condyles (larger neural canals and smaller condyles in ATV); zygapophyses that project laterally (zygapophyses more in line with long axis of centrum in ATV); and anteroposteriorly elongation (dorsoventrally expanded in ATV) (Holman, 1979, 1981b; Rage, 1988; LaDuke, 1991).

Family Viperidae Oppel, 1811

Genus and Species Indeterminate

Referred material. ─ LSUMG V-21172, 21173, 21207, 9117, four vertebral centra from the Stonehenge site.

Description. ─ LSUMG V-21172 consists of a centrum with a well-developed, ventrally projecting hypapophyses that is greater than one third the thickness of the condyle. The hypapophysis of LSUMG V-21173 is broken just above the ventral border of the centrum; however, like LSUMG V-21172, the thickness at the breakage is greater than one third the thickness of the condyle.

Discussion. ─ Even with the fragmentary nature of these vertebrae, they are readily identifiable as members of the viper family based on hypapophyses that are greater than one-third the width of the condyle, the robust condyle, and general robust form of the vertebrae (Holman, 1979 and 2000; Parmley and Holman, 1995). Unfortunately, the fragmentary nature of these vertebrae does not allow assignment to subfamily or genus at this time.

The earliest record of the family Viperidae in North America is from the late Arikareean Mouth of McCann's Canyon site in Cherry County, Nebraska with an indeterminate genus and species of viperid (Holman, 1981; 2000). In addition, an indeterminate genus and species of viperid is also known from the early Barstovian of east Texas (Holman, 1966; 1977; 1996; 2000). The occurrence of the family Viperidae in Louisiana during the middle Barstovian is not unexpected, and their presence in Louisiana adds insight into the early evolutionary history and biogeography of the family.

Family, Genus, and Species indeterminate

Referred material. ─ LSUMG V- 21278, 21279, 21280, 21281 21283, 21285, 21287, seven ATV from the Stonehenge site; LSUMG V-21282, 21284, 21288, 21289, four fragmentary vertebrae from the Stonehenge site.

Description/Discussion. ─ The ATV have ventrally projecting hypapophyses on the centrum and large neural canals and small condyles when preserved. They are also anteroposteriorly forshortened and dorsoventrally elongated. The four fragmentary vertebrae are colubrid based on the light overall build, thin neural spines and hemal keels, and small synapophyses; however, they are too fragmentary to assign to subfamily or below.

Family, Genus, and Species indeterminate

Referred material. ─ LSUMG V-4038, 9122, 9123, 21101, 21102, 21103, 21104, 21105, 21106, 21107, 21108, 21109, 21110, 21111, 21112, 21113, 21114, 21115, 21116, 21117, 21118, 21119, 21120, 21121, 21122, 21123, 21124, 21125, 21126, 9145, 21128, 9143, 32 postcloacal (caudal) vertebrae from the Stonehenge site; LSUMG V-12776, 21265, 21266, 21267, 21268, 21269, 21270, 21271, 21272, 21273, 21274, 11fragmentary vertebrae from the Stonehenge site; LSUMG V-21190, 21199, 21200, 21201, four caudal vertebrae from the TVOR site; LSUMG V-21202, 21203, 21204, 21206, four fragmentary vertebrae from the TVOR site; LSUMG V-21224, one fragmentary vertebra from the TVOR Southeast site; LSUMG V-21216, V-21220; two fragmentary vertebral centra from the TVOR Southeast site; LSUMG V-21217, 21218, 21219, 21227, four cervical vertebra from the TVOR Southeast site; LSUMG V-10892, one cervical vertebra from the TVOR North Creek site; LSUMG V-21215, one caudal vertebra from the TVOR North Creek site; LSUMG V-21238, 21239, two fragmentary vertebrae from the TVOR North Creek site; LSUMG V-9925, one caudal vertebra from the Gully site.

Description. ─ The caudal vertebrae are characterized by remnants of the broken hemapophyses that would have extended ventrally from the centrum, and complete left and broken right pleurapophyses on ventrolateral surface.

Discussion. ─ Ophidian caudal vertebrae are typically divided into cloacal and postcloacal regions based on the double-keeled hemapophyses and pleurapophyses of postcloacal vertebrae and lymphapophyses found on cloacal vertebrae. Unfortunately, caudal vertebrae have not proven to be sufficiently diagnostic to the generic or specific level (LaDuke, 1991; Holman, 2000), so no taxonomic determinations based on caudal vertebrae have been attempted herein.

Tunica Hills/Kerry Faunal List

Clays from the TunicaHills/Kerry locality are currently being sieved, with new specimens being recovered (Dr. Schiebout Pers. Comm.). A preliminary faunal list is presented here, awaiting new material from the sieving efforts.

Class Amphibia Linnaeus, 1758

Superorder Salientia Laurenti, 1768

Order Anura Rafinesque, 1815

Family Ranidae Gray, 1825

Genus Rana Linnaeus, 1758

Class Reptilia Laurenti, 1768, emend. Gauthier, Kluge, and Rowe, 1988

Order Squamata Oppel, 1811

Suborder Serpentes Linnaeus, 1758

Family Colubridae Oppel, 1811

Subfamily Natricinae Bonaparte, 1840

Discussion

The modern East and Gulf Coast distribution of the salamander, *Siren*, was in place by at least the Hemingfordian with the appearance of *Siren hesterna* from Gilchrist County, Florida. Holman (2006) noted that the presence of the Eocene taxon, *Siren dunni*, from Wyoming and the discovery of *Siren* sp. from Nebraska "nicely fill in the gap between Texas and Wyoming in the fossil record of this genus". The geographic distribution of *Siren* appears to have been shrinking in the Cenozoic, probably a result of the cooling climate and lack of quiet, still waters in warm humid environments.

The presence of the salamanders, *Siren miotexana* and *Notophthalmus slaughteri* from Fort Polk is only the second documentation of these species in the fossil record. Their occurrence at Fort Polk adds an eastern geographic range extension of approximately 143 miles and a temporal range extension of about 2.5 million years.

With the exception of extreme southwestern Louisiana, the modern range of the salamander, *Notophthalmus*, includes much of the eastern United States including most of Louisiana and eastern Texas (Conant and Collins, 1998), so the presence of the genus in the Middle Miocene of eastern Texas and west-central Louisiana does not present an extralimital occurrence.

Judging from the distribution of *Batrachosauroides* from the Early to Middle Miocene, it was a Gulf Coast endemic, as no specimens are known from the heavily sampled High Plains localities in Nebraska and South Dakota. The presence of *Batrachosauroides gotoi* from the early Eocene of North Dakota establishes the presence of the genus in more northern latitudes around the Early Eocene Climatic Optimum, a time of much warmer global temperatures and presumably greater precipitation than the area now receives. The lack of *Batrachosauroides* during the Oligocene could be the result of two factors: 1) the general cooling during the

Oligocene drove populations farther south, where heat and rainfall were in abundance, or 2) there are few Oligocene herpetofaunal-bearing exposures east of the Rockies with adequate sampling for microvertebrates. While the latter point is true when one compares Oligocene to Miocene localities, I believe the deteriorating climate during the Oligocene played a major role in restricting *Batrachosauroides* to the hot and humid Gulf Coast during the Miocene. After the Middle Miocene Climatic Optimum, about 16 mya, the rapidly cooling climate created a hostile environment for *Batrachosauroides*.

Modern *Acris* have a range covering most of the eastern United States, east of the Rocky Mountains (Conant and Collins, 1998). *Acris* appear to have been wide-ranging by the time of their first appearance in the Hemingfordian of North America, covering an area from the eastern foothills of the modern Rocky Mountains to almost the east coast of Florida, which suggests a much earlier arrival or diversification of the genus in North America. All Miocene records of the genus fall within this range.

The treefrog, *Hyla miocenica*, is only known from the east Texas and west Louisiana Gulf Coast. Unless specimens are recovered from other localities outside the area, it will be assumed that *Hyla miocenica* evolved on the Gulf Coast and did not migrate far from the immediate Gulf Coast of east Texas and western Louisiana before going extinct in the late Barstovian.

The extinct toad species, *Bufo hibbardi*, was locally abundant in Nebraska by the earliest occurrence of the taxon in the middle Barstovian, suggestive of a speciation event in Nebraska, with a fairly rapid (~2.5 million years) southward dispersal into Louisiana by the late Barstovian. As underwater screening of sediments of the Hemphillian TunicaHills/Kerry locality in Louisiana continues, it will be interesting to see if *Bufo hibbardi* was part of the fauna, remaining on the Gulf Coast, or retreated back northward before its extinction in the Late Miocene.

The presence of the snake, ?*Boavus affinis*, from the early Barstovian of the Texas Gulf Coast and *Boavus* cf. *Boavus affinis* from Fort Polk is of considerable biogeographic interest. If these records are correct and do not represent a separate Gulf Coast species of *Boavus*, then *Boavus affinis* must have migrated from California to the Gulf Coast via a southern route, as the culmination of the Laramide Orogeny in the Eocene would have presented a formidable barrier if a more northern route was taken. Furthermore, there are no records of *Boavus affinis* from the well-sampled Arikareean, Hemingfordian, and Barstovian Great Plains localities. The Louisiana record of *Boavus* cf. *Boavus affinis* presents temporal and geographic range extensions of about 2.5 million years and approximately 143 miles, respectively.

The presence of three late Arikareean Great Plain's localities at roughly equivalent latitudes containing the snake, *Ogmophis miocompactus*, and an early Hemingfordian record along the same transect implies a center of distribution in the region. Admittedly, there is a dearth of late Arikareean localities with fossil snake remains south of the aforementioned localities, Toledo Bend being the only locality on the central Gulf Coast (Holman, 2000). Albright (1994) reported "near *Ogmophis* sp." from the Toledo Bend locality that was subsequently called cf. *Ogmophis* sp. by Holman (2000). The lack of Barstovian *Ogmophis miocompactus* records in the majority of Great Plains localities (zero out of 15 in Nebraska and one out of two in South Dakota) suggests it was no longer a key component of the ecosystem, due to changing habitats, competition from colubrid snakes, or both.

The archaic colubrine snake, *Ameiseophis robinsoni*, was restricted to Wyoming by its first appearance in the late Arikareean. The greatly expanded longitudinal range during the Hemingfordian does not allow for the determination of any distributional centers. One could suggest that the species originated in the vicinity of Wyoming because of the Arikareean and

Hemingfordian records, but because these records are from different stratigraphic horizons within the same locality, this assertion is tenuous. The presence of *Ameiseophis* cf. *Ameiseophis robinsoni* from the Fort Polk locality represents a significant, southern range increase for a northern occurring taxon.

Because the middle Barstovian distribution of the snake *Nebraskophis skinneri* is restricted to two northern Nebraska localities, and subsequent late Barstovian occurrences are south of them, it is probable that *Nebraskophis skinneri* evolved in the Great Plains and then migrated southward through the middle Barstovian and beyond. The middle Hemphillian record in southwestern Nebraska implies that the population grew southward and either remained in Nebraska since its inception, or retreated south of Nebraska after the middle Barstovian, then returned sometime before the middle Hemphillian. The Fort Polk record of *Nebraskophis skinneri* represents a significant southern extension of its geographic range, making it the southernmost record of this taxon during its phylogenetic history.

The early Hemingfordian records of the snake, *Salvadora paleolineata*, imply a northern Nebraska or southern South Dakota center of distribution. Within the three million year time span between the early Hemingfordian and the early Barstovian, *Salvadora paleolineata* had spread west into Wyoming and south to the Texas Gulf Coast and remained in the area between the Appalachian and Rocky Mountains for the duration of its geologic range, until its extinction in the middle Hemphillian.

The first appearance of the natricine snake, *Neonatrix elongata*, in the early Hemingfordian of South Dakota might suggest an origin in that area, but caution must be used, as it is one of only two Hemingfordian localities in the area, and with the exception of the Thomas Farm locality on the Florida peninsula, there are none on the Gulf Coast. Whether *Neonatrix elongata* existed on

the Gulf Coast before the early Barstovian cannot be ascertained given the data from the fossil record, but by the early Barstovian, it was definitely present on the Texas Gulf Coast. By the middle Barstovian the geographic range of *Neonatrix elongata* had expanded to include a large portion of the central United States from the Gulf Coast to southern South Dakota.

Summary

In general the North American snake fauna can be divided into four biogeographic zones: (1) the west coast, (2) the Great Plains, (3) Gulf Coast, and (4) Florida, and the east coast. The Gulf Coast and Great Plains faunas are similar enough in their faunal compositions to be included together except for *Batrachosauroides*, which was endemic to the Gulf Coast. Apparently, taken together, the Great Plains and Gulf Coast, being sandwiched in between the Rocky and Appalachian mountains, was isolated enough and underwent significant enough climatic, floristic, and faunal changes through the Miocene to produce extinct and extant lineages of snakes.

CHAPTER 3: BIOSTRATIGRAPHY OF NEOGENE OPHIDIANS

Introduction

Due to the belief that fossil reptiles and amphibians evolve slowly, fossil snakes are rarely used to answer stratigraphic questions. However, compared to other reptile groups, snakes have evolved quite rapidly (Romer, 1966). While the grasses were spreading and the horses were radiating throughout North America during the Miocene, there was a concomitant burst of evolution within certain snake lineages, with more derived colubrid taxa displacing the more ancient boids in North America and Europe (Holman, 1976a, 1976b, 2000).

The idea of fossil snakes being used biostratigraphically was first proposed by Holman (1976a and 1976b) when he demonstrated that Early Miocene localities contain a preponderance of henophidian and archaic colubrid genera (ancient caenophidian taxa), Middle Miocene localities contain roughly equal numbers of henophidian and caenophidian snakes, and Late Miocene localities are dominated by modern caenophidian snakes. According to the classification scheme of Underwood (1967) there are three superfamilies of snakes. The scolecophidia consists of primitive, blind, burrowing snakes that are rare in the fossil record because of their diminutive size. The henophidians are the primitive boids and pythons that usually have vestigial hind limbs present. The caenophidians are modern snakes that do not have vestigial hind limbs. With the exception of the Early Eocene I-75 site in Florida (Holman, 1999), the Early Eocene Hardie Mine local fauna in Georgia (Parmley and Holman, 2002), and the Flats locality in eastern Colorado (Holman, 1984, 2000), North American Paleogene snake faunas consist of only henophidian snakes. The oldest known North American colubrid snake is an indeterminate species of *Nebraskophis* from the Late Eocene (Jacksonian= Priabonian Stage) of central Georgia (Parmley and Holman, 2002).

Holman (1976a) entertained the possibility of using snakes to subdivide the Miocene and tested the hypothesis using data from four Great Plains localities spanning the Miocene. His results were encouraging, though, prior to this study, no subsequent work has been done incorporating snake data from other Miocene sites across North America. This study will expand upon the preliminary data of Holman (1976a), attempt to test it, and endeavor to use individual species to subdivide the Miocene Epoch.

Methods

Fossil snake faunal compositions were tabulated for 21 previously-studied North American sites spanning the Miocene and for the Fort Polk herpetofauna (Figure 3-1). Individual taxon stratigraphic ranges were put into Excel then graphed by NALMA to produce a composite stratigraphic section for North America. When gaps in stratigraphic ranges were present, they were included as part of the taxon's temporal range to produce a plot of the total temporal range of the taxon. Numerical ages were extracted from Tedford *et al.* (1987, 2004) and Holman (2000) when the original publication did not provide one. Specimens identified as "cf." to a species were included in this study because many fossil snakes have been identified in this manner. Furthermore, taxa known from only one locality (like most from the Hemingfordian Thomas Farm locality in Florida), and thus having severely limited temporal and geographic ranges, were excluded from this study and are only mentioned in the site descriptions for completeness. The following sites were used in compiling data for figure 3-1 and include snake taxa from the Miocene to the recent.

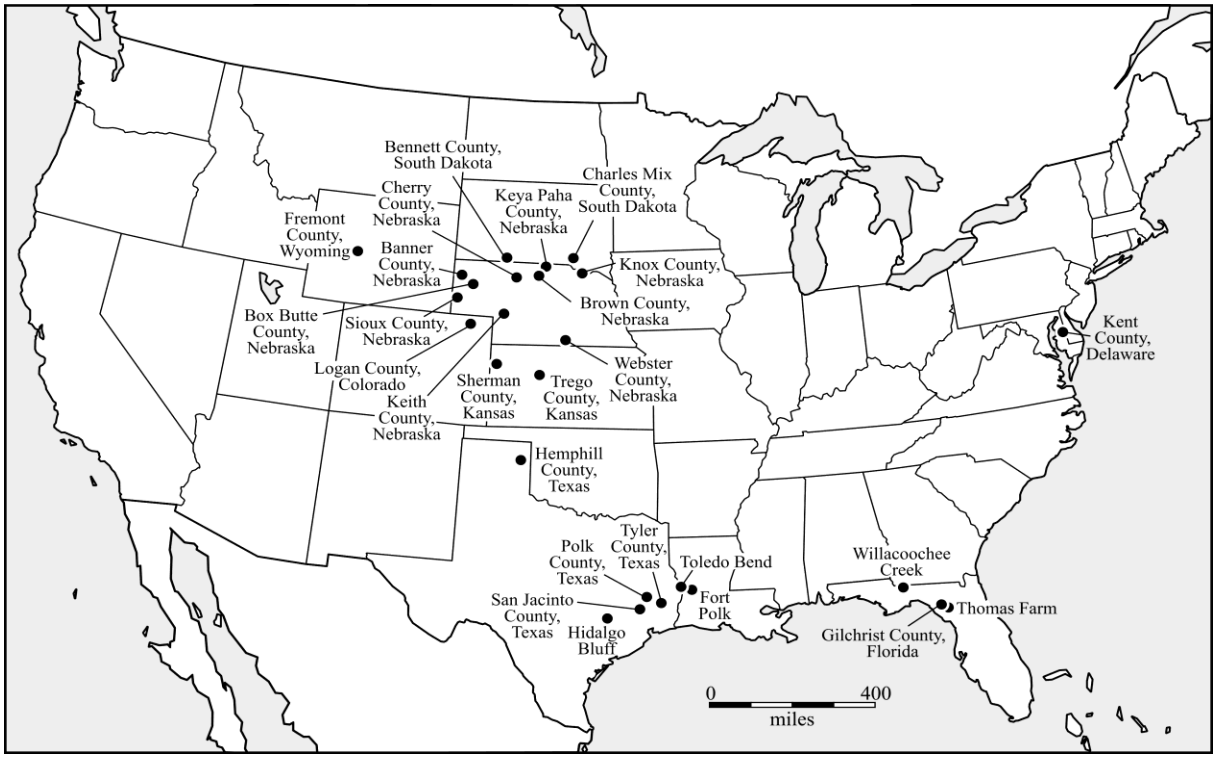

Figure 3-1. Miocene North American herpetofaunal-bearing localities.

Late Arikareean Localities (24-19 Ma)

The Toledo Bend Site

The Toledo Bend Site is located in east Texas on the Sabine River and represents a rare glimpse into this time period on the Gulf Coast. This site is within the Carnahan Bayou Member of the Fleming Formation (Figure 4), and based on mammalian biostratigraphy, corresponds with the late Arikareean Land Mammal Age of Woodburne (2004)(Albright, 1991, 1994). Albright (1994) reported on the lower vertebrates from the site, which includes two henophidian taxa. The first is one vertebra of an unknown genus and species of erycine boa. The second consists of five vertebrae referred to *Anilioides nebraskensis,* which is a non-erycine boa.

Armstrong Ranch Quarry and Lizard Quarry

Both of these sites are part of the Harrison Formation in Sioux County, Nebraska. Holman

(1977a) described a new species of erycine boa (*Geringophis yatkolae)* from the Lizard Quarry from one well-preserved trunk vertebra. Holman (1977a) described two additional trunk vertebrae from this quarry as *Ogmophis* cf. *Ogmophis miocompactus.* In addition to these henophidian taxa, Holman (1977a) described one indeterminate colubrid vertebra from the Lizard Quarry site.

The Armstrong Ranch Quarry yielded two specimens of the henophidian *Ogmophis* cf. *Ogmophis miocompactus* (Holman, 1977a). No caenophidian taxa were recovered.

Gering Formation Sites

Five extinct henophidian species have been recovered from the Early Miocene Gering Formation sites in Nebraska (Holman, 1976b). Within the family Boidae, ten trunk vertebrae were identified as belonging to the erycine boid *Calamagras platyspondyla,* four trunk vertebrae were assigned to the erycine boid *Calamagras angulatus,* and three trunk vertebrae were identified as *Geringophis depressus.* In addition, eleven trunk vertebrae were identified as *Anilioides nebraskensis,* the only representative of the family Aniliidae. Finally, Holman (1976b) named the new genus and species of snake, *Goinophis minusculus,* which is from an indeterminate family, but definitely a henophidian snake.

Monroe Creek Formation

Fossil Snakes collected from the Monroe Creek Formation, Goshen County, Wyoming are considered Arikareean in age (Holman, 1977b). Holman (1977b) identified three erycine boids and one aniliid snake, all of which are henophidians. The erycine taxa included two trunk vertebrae from *Calamagras* cf. *C. angulatus*, one trunk vertebra belonging to *Calamagras*

platyspondyla, and one trunk vertebra identified as *Geringophis depressus.* Only one aniliid trunk vertebra was recovered, which was assigned to *Anilioides nebraskensis.*

Split Rock Formation Lower Unit

The Split Rock Formation consists of four sites that are located in central Wyoming, and have been divided into a lower unit that is Early Miocene (late Arikareean) and an upper unit that is late Middle to Late Miocene (Holman, 1976c, 2000). Tedford *et al*. (2004) consider the Split Rock Formation fauna to represent the late Hemingfordian, which is the age used herein for the upper unit. Holman (1976c) described the fossil snake fauna from the upper and lower units and identified three henophidian and three caenophidian taxa from the lower unit. The henophidian taxa included the erycine boas *Calamagras weigeli, Ogmophis* cf. *Ogmophis miocompactus*, and *Charina prebottae*. The caenophidian taxa consisted of taxa from the natricine and colubrine subfamilies of the Colubridae. The natricine was identified as natricine indeterminate, and the colubrines included *Ameiseophis robinsoni* and *Pseudocemophora* cf. *Pseudocemophora antiqua.*

Hemingfordian Localities (19-16 Ma)

Black Bear Quarry II

The Black Bear Quarry II is located in the Rosebud Formation of Bennett County, South Dakota. The site has been assigned a Land Mammal Age of Hemingfordian (Holman, 1976). Holman (1976d) described four henophidian boids and three caenophidian colubrids from the site. The boids are all members of the subfamily Erycinae and include twelve *Ogmophis miocompactus* trunk vertebrae, two trunk vertebrae from *Calamagras weigeli*, six *Charina*

prebottae trunk vertebrae, and three trunk vertebrae from *Pterygoboa miocenica*. Both natricine and colubrine subfamilies of the Colubridae are known from this site. The only natricine representative is a trunk vertebra from *Neonatrix elongata.* On the other hand, the colubrines are represented by six *Salvadora paleolineata* trunk vertebrae and one trunk vertebra from *Dakotaophis greeni*, which represents a new genus and species.

Marsland Quarry

The Marsland Quarry in Box Butte County, Nebraska, is early Hemingfordian (Tedford *et al.* 1987; Holman, 2000), and contains the following fossil snakes: *Charina prebottae*, *Dakotaophis greeni*, and *Salvadora paleolineata* (Holman, 1977, 1979, 2000).

Split Rock Formation Upper Unit

Holman (1976c) identified the snake taxa from the upper unit of the Split Rock Formation, which included three henophidians and seven caenophidians. The upper unit was reported by Holman (1976b, 2000) to range from middle Hemingfordian to late Barstovian and is herein referred to the late Hemingfordian, as the snake fauna are more indicative of the Hemingfordian, as all colubrine genera, with the exception of *Salvadora paleolineata*, are considered archaic colubrids by Holman (2000). The Upper unit included one henophidian and five caenophidians. The henophidian was identified as *Charina prebottae.* The caenophidian taxa were all colubrines and included *Ameiseophis robinsoni*, *Dakotaophis greeni*, *Paracoluber storeri*, *Pseudocemophora* cf. *Pseudocemophora antiqua*, and *Salvadora paleolineata*.

Thomas Farm Locality

The middle Hemingfordian Thomas Farm Locality is located in Gilchrist County, Florida (Auffenberg, 1963). There are three henophidian taxa and three caenophidian taxa known from the site (Auffenberg, 1963; Holman, 2000). The henophidian taxa include *Anilioides minuatus, Calamagras floridanus,* and *Ogmophis pauperrimus, Pseudoepicrates stanolseni*; the caenophidian taxa are represented by *Paraoxybelis floridanus,* and *Pseudocemophora antiqua.* It was decided by Holman (2000) that *Ogmophis pauperrimus* should be a nomen dubium, as he determined the vertebrae to be from an indeterminate colubrid rather than boid snakes.

Early Barstovian Localities (16-15 Ma)

Trinity River Site

The Trinity River Site is part of the Fleming Formation and is located near Coldspring, Texas. The fossil herpetofauna from this site was first reported by Holman (1966) with addendums in 1977, 1979, and 1996 (Holman, 1977c, 1979). Two henophidian taxa were identified as *Boavus affinis,* a boine boid, and *Ogmophis miocompactus,*an erycine boid. The caenophidian taxa include the colubrines *Dakotaophis greeni, Salvadora paleolineata, Texasophis fossilis,* the natricines *Neonatrix elongata*, *N. infera,* and one indeterminate viperid.

Livingston Dam Site

Located in southern Polk County, Texas, and part of the Fleming Formation, the Livingston Dam Site yielded one trunk vertebra from an indeterminate genus and species of boid from the subfamily Boinae (Holman, 1977c).

Town Bluff Site

The Town Bluff Site is also part of the Fleming Formation of east Texas, and is located in Tyler County, Texas. Holman (1977, 1991) reported three colubrine and one natricine colubrid snakes from the site. The colubrines included *Elaphe kansensis, Salvadora paleolineata,* and *Texasophis fossilis*; the natricine snake was *Neonatrix infera*.

The Moscow Site

The Moscow Site is part of the Fleming Formation and is located in northern Polk County, Texas. Holman (1977c) identified one erycine boa, one colubrine, and one natricine snake from the site. The erycine boa was *Calamagras weigeli,* the colubrine *Elaphe kansensis,* and the natricine *Neonatrix elongata*.

Middle Barstovian Localities (15-14 Ma)

Norden Bridge Site

Located in Brown County, Nebraska, the Norden Bridge Site contains a diverse assemblage of fossil snakes. The henophidians recovered are *Charina prebottae* and *Geringophis depressus*, while the colubrid fauna contains *Paleoheterodon tiheni, Ameiseophis* cf. *Ameiseophis robinsoni, Elaphe kansensis, Lampropeltis similis, Nebraskophis skinneri, Salvadora paleolineata, Neonatrix elongata, Neonatrix magna,* and an indeterminate viperid (Holman, 2000).

Kleinfelder Farm Locality

The Kleinfelder Farm Locality in Saskatchewan, Canada, is part of the Wood Mountain Formation, and is the only Miocene locality in Canada to produce fossil snakes (Holman, 2000).

Fossil snakes from this locality include the erycine boid, *Charina prebottae* and the colubrids *Elaphe kansensis*, *Lampropeltis similis*, and *Paracoluber storer* (Holman, 1970, 1979, 2000).

Late Barstovian Localities (14-12.5 Ma)

Fort Polk Sites

The Fort Polk sites are within the Castor Creek Member of the Fleming Formation and are considered early late Barstovian in age (Schiebout and Ting, 2000, Schiebout *et al*, 2004; Williams and Schiebout, 2004). The henophidians from Fort Polk include *Boavus* cf. *Boavus affinis*, an indeterminate species of *Calamagras* and ?*Ogmophis miocompactus*. The colubrids *Ameiseophis* cf. *Ameiseophis robinsoni, Salvadora* cf. *Salvadora paleolineata, Nebraskophis* cf. *Nebraskophis skinneri,* and *Neonatrix elongata* have been described from the locality.

Myers Farm Site

The speciose Myers Farm Site is located in Webster County, Nebraska. Holman (1977d) described two henophidians and nine caenophidians from the site. The henophidians included *Geringophis depressus* and *Pterygoboa miocenica*, while the caenophidian fauna consisted of *Paleoheterodon tiheni, Elaphe kansensis, Nebraskophis skinneri, Salvadora paleolineata, Neonatrix elongata, Nerodia* sp., *Thamnophis* sp., *Micrurus* sp., and an indeterminate crotaline.

Clarendonian Localities (12.5-9 Ma)

WaKeeney Local Fauna

The Clarendonian WaKeeney Local Fauna in Trego County, Kansas contains a diverse ophidian assemblage consisting of mostly caenophidian snakes. The henophidians described

from the site are *Ogmophis pliocompactus* and *Tregophis brevirachis* (Holman, 1975, 2000). The caenophidian fauna is comprised of six taxa: *Paleoheterodon* sp. indeterminate, *Masticophis* or *Coluber*, a species of *Elaphe*, *Lampropeltis similis*, *Texasophis wilsoni*, *Nerodia hillmani*, and an indeterminate species of *Thamnophis* (Holman, 1975, 2000).

Hemphillian Localities (9-5 Ma)

Haile VIA Locality

The late Miocene (Hemphillian) Haile VIA Locality is located in Alachua County, Florida. Auffenberg (1963) reported on the fossil snakes from this locality, of which only caenophidians were found, including *Diadophis elinorae, Heterodon brevis, Stilosoma vestustum,* and a species of *Micrurus*.

Higgins Local Fauna

The Higgins Local Fauna is found in Lipscomb County, Texas. The locality is considered early Hemphillian (Parmley and Holman, 1995; Holman, 2000; Tedford *et al*., 2004). The fossil snakes from this locality include one henophidian and four caenophidian taxa (Parmley and Holman, 1995; Holman, 2000). The henophidian is *Charina prebottae,* and the caenophidians include *Paleoheterodon tiheni, Coluber* or *Masticophis, Miocoluber dalquesti,* and *Thamnophis* cf. *proximus* or *sirtalis.*

Mailbox Prospect

The Mailbox Prospect site is in Antelope County, Nebraska and is Late Miocene age (late Hemphillian) (Parmley and Holman, 1995; Holman, 2000). The fauna are composed of all

caenophidian snakes and includes *Heterodon platirhinos, Paleoheterodon tiheni, Elaphe guttata, Coluber* or *Masticophis, Lampropeltis triangulum, Pituophis melanoleucus, Nerodia* sp., *Thamnophis* sp., and *Crotalus* sp. (Parmley and Holman, 1995; Holman, 2000).

Discussion

Figure 3-2 shows the stratigraphic position of most North American fossil ophidians from the Late Oligocene to the present. The Late Oligocene through Early Miocene (Arikareean) is completely dominated by henophidian snakes, many of which are boids and holdovers from the Oligocene and earlier (Figure 3-2; Holman, 2000). One hundred percent of North American snakes from the selected localities up to the early Hemingfordian, at 19 Ma, are henophidians. Beginning in the late Arikareean to early Hemingfordian, about 19 Ma, the North American snake fauna began to change from henophidian (mostly boid) dominated faunas to one in which colubrids were key a component, representing the first appearance of the colubrids *Dakotaophis greeni, Salvadora paleolineata, Neonatrix elongata,* and *Ameiseophis robinsoni* (Figure 3-2; Holman, 2000) that comprised 40% of the North American ophidian fauna. Along with the first appearance of the aforementioned colubrids, were the first appearances of two erycine boids, *Pterygoboa miocenica* and *Charina prebottae* (Figure 3-2; Holman, 2000). Between 18 and 17 Ma, *Pseudocemophora antiqua* originated and went extinct, and in the early Barstovian, *Dakotaophis greeni* went extinct (Figure 3-2; Holman, 2000).

The Barstovian in many localities across North America was exemplified by a diverse assemblage of ancient boids and modern colubrids. During the early Barstovian, the displacement of henophidian taxa by caenophidians continued. At this time there were equal numbers of henophidian and caenophidian taxa (Figure 3-2).

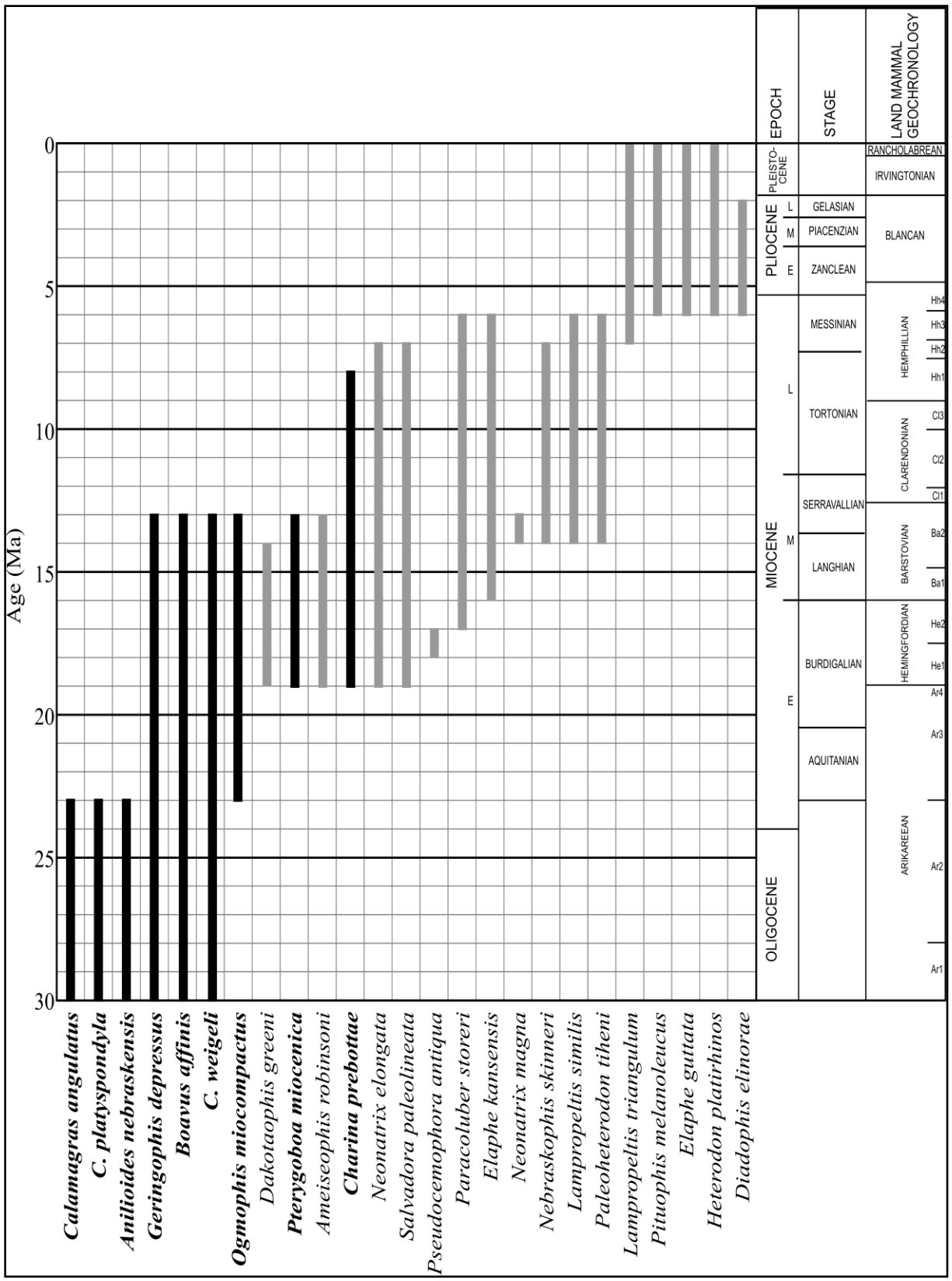

Figure 3-2. Composite stratigraphic ranges for North American snake taxa. Age (Ma), Epochs, and Stages from Lourens *et al*. (2004). Boids are shown in Bold.

The first record of *Elaphe kansensis*, from the Town Bluff and Moscow Landing localities on the Texas Gulf Coast, occurred at 16 Ma (Figure 3-2; Holman, 2000). The middle Barstovian (14 Ma) saw the origination of four new colubrid taxa: *Neonatrix magna*, *Nebraskophis skinneri*, *Lampropeltis similis*, and *Paleoheterodon tiheni* (Figure 3-2; Holman, 2000), which moved the caenophidian abundance to 60% and henophidian to 40%. Finally, figure 29 illustrates an extinction event at the end of the Barstovian for a handful of colubrids and boids, including *N. magna* and *Ameiseophis robinsoni* of the Colubridae and the boids *Ogmophis miocompactus*, *Calamagras weigeli*, *Boavus affinis*, and *Geringophis depressus*. The late Barstovian percent henophidian abundance dropped to approximately 33%. There are two henophidian genera described from late Barstovian Fort Polk herpetofauna, which compose 33% of the snake fauna.

With the exception of the previously mentioned extinctions toward the end of the Barstovian, Clarendonian ophidian faunas were similar to Barstovian, as there were no speciation, extinction, or immigration events recorded in the fossil record of these faunas during the Clarendonian (Figure 3-2). The Hemphillian, on the other hand has two extinction events: one at 7 Ma and the other at 6 Ma (Figure 3-2). The older event included the disappearance of *Neonatrix elongata*, *Salvadora paleolineata*, and *Nebraskophis skinneri* while the younger one was characterized by the last occurrences of *Paracoluber storeri*, *Elaphe kansensis*, *Lampropeltis similis*, and *Paleoheterodon tiheni*.

Snake Biostratigraphy

During the Barstovian, between 16 and 12.5 Ma, colubrids populations expanded while boids contracted. By the late middle Barstovian, colubrid snakes were dominated by boid snakes for the first time in earth history. The only North American boids to survive beyond the

extinction event at the end of the Barstovian were erycines, *Ogmophis pliocompactus*, *Tregophis brevirachis*, and *Lichanura* sp. (all not shown in Figure 3-2 because of restricted geographic ranges), and *Charina prebottae* (Figure 3-2; Holman, 2000).

At first glance, the composite section for North American Miocene snake taxa looks promising for subdividing the Late Oligocene and Miocene, but there are problems. First, *Calamagras platyspondyla* and *Anilioides nebraskensis* could be used to recognize the Arikareean, because their stratigraphic ranges span it, and it is important to note that these taxa are found from several localities, which greatly enhances their utility. But, *Calamagras angulatus* has a total temporal range from the Early Oligocene to the Early Miocene, a span of approximately eight million years, which is too long to be of great stratigraphic use. The last appearance of *Calamagras angulatus*, *C. platyspondyla*, and *Anilioides nebraskensis* coupled with the first appearance of *Ogmophis miocompactus* could be used as an indicator for the late Arikareean. While *Ogmophis miocompactus* spans the Early Miocene to Middle Miocene, and it is found in several localities over a wide geographic range, it is not useful because the relatively long stratigraphic range of approximately ten million years precludes this. On the plus side, *Pterygoboa miocenica* and *Dakotaophis greeni* can be used as a concurrent range zone to subdivide the upper Lower Miocene to late Middle Miocene because of their wide geographic range, narrow stratigraphic range, and abundance in several localities.

Pseudocemophora antiqua appears to be a decent Hemingfordian indicator, as its short temporal and wide geographic ranges indicate. However, the large geographic range, spanning central Florida to western Wyoming, with no confirmed identifications in between, and the tentativeness of *Pseudocemophora* cf. *Pseudocemophora antiqua* identifications for the Wyoming specimens, argue against this. In fact, in regards to the identity of the Wyoming

specimens, Holman (2000) states “Because of the wide geographic separation of the two fossil occurrences and because no other fossil records of the genus or species occur in the literature, the Wyoming records should be regarded with some degree of caution.”

The short stratigraphic range of *Neonatrix magna*, which occurred between 14 and 13 Ma, is similar in duration to *Pseudocemophara antiqua*. Furthermore, it appears in more than one locality, but has a limited geographic extent with all the localities occurring in Nebraska.

The first appearances of the colubrids *Dakotaophis greeni*, *Salvadora paleolineata*, *Neonatrix elongata*, and *Ameiseophis robinsoni* and the boids, *Pterygoboa miocenica* and *Charina prebottae* in the early Hemingfordian are provocative. These taxa have been described from multiple localities in North America, and as such, have the potential to be biostratigraphically useful as early Hemingfordian indicators. However, because of their long stratigraphic ranges which hinder precise placement within the late Early to Middle Miocene, their utility would be restricted to supplementing other biostratigraphic proxies, such as mammalian biostratigraphy or paleomagnetic data,. Taken by itself, *Dakotaophis greeni*, with its short stratigraphic range, commonness in the fossil record, and widespread occurrence can be used to recognize the Hemingfordian to early Barstovian.

The extinction of *Geringophis depressus*, *Boavus affinis*, *Calamagras weigeli*, *Ogmophis miocompactus*, *Pterygoboa miocenica*, *Ameiseophis robinsoni*, *and Neonatrix magna* at the end of the Barstovian is of considerable interest. The use of these taxa as indicators of the Barstovian-Clarendonian boundary along with mammalian data is possible.

The problem of taxa appearing at only one site, and thus, apparently having a very short stratigraphic range, occurs in a few localities. *Geringophis yatkolae* has a very short stratigraphic range, but this is due to it only appearing at the Early Miocene Lizard Quarry in Nebraska.

Anilioides minuatus, *Calamagras floridanus*, *Pseudoepicrates stanolseni*, and *Paraoxybelis floridanus* all appear to have a short stratigraphic range, but they are only known from the Thomas Farm locality in central Florida. Finally, *Elaphe guttata*, *Lampropeltis triangulum*, and *Pituophis melanoleucus* are all extant taxa.

The trend of henophidian taxa being outcompeted by caenophidian invaders during the late Early to Middle Miocene, as suggested by Holman (1976a, 1976b, 2000), is evident in Figure 3-2. The fast radiation and colonization of colubrid snakes in North America is considered "one of the most rapid evolutionary radiations of any vertebrate group" (Holman, 2000). This is similar to a trend seen in fossil horses at this time, in which there is an "explosion" of hypsodont horses in the fossil record, apparently responding to the increase in silica-rich grasses as the dominant vegetation (Macfadden, 1991). Whether the fossil snakes are responding to the spread of grasslands cannot be ascertained, but the timing of the explosion is suggestive. Holman (2000) argued that the coevolution of grasslands, rodents, passerine birds, and colubrine snakes might have been the stimulus for the colubrid radiation in North America. Furthermore, he suggested the possibility of direct competition between colubrine snakes during the Middle Miocene, as some modern colubrines feed upon other snakes (Holman, 2000).

The percent abundance of henophidian taxa decreased throughout the Miocene of North America in concert with an increase in caenophidian taxa as was suggested by Holman (1976a, 1976b, 2000). Ratios of caenophidians and henophidians can be used to coarsely subdivide the Miocene, as Arikareean faunas contain almost 100% henophidians, early Hemingfordian faunas contain approximately 60% henophidians, early Barstovian faunas contain approximately 50% henophidians, middle Barstovian approximately 40% henophidians, and late Barstovian approximately 33%. For instance, taxonomic compositions of five henophidians to one

caenophidian would surely be Early Miocene in age, whereas, a composition of five caenophidians to one henophidian would undoubtedly be Late Miocene. The faunal snake composition from the late Barstovian Fort Polk locality is indicative of a late Barstovian age, as the fauna contains 33% henophidian taxa.

The use of snakes in terrestrial biostratigraphy is not as powerful as their mammalian contemporaries because of longer temporal ranges and a lack of diversity. For example, *Dakotaophis greeni* is indicative of Hemingfordian to early Barstovian strata. Data from new sites will further enhance this biostratigraphic tool. Due to the coarse nature of using fossil snakes as biostratigraphic markers, they are best used in conjunction with other data sets such as mammals and pollen to answer biostratigraphic questions.

CHAPTER 4: PALEOENVIRONMENTAL RECONSTRUCTIONS

Introduction

Fossil amphibians and reptiles are often one of the best means of reconstructing ancient habitats. For instance, the presence of frogs, freshwater turtles, crocodilians, and natricine snakes at a fossil locality suggests a depositional environment with permanent water sources such as slow-moving creeks, floodplains, and lakes, and as such, is a suitable means of determining paleoenvironments. This type of qualitative paleoenvironmental interpretation, based on the herpetofaunal makeup, is useful and will be utilized in this dissertation. However, with well-sampled localities containing large numbers of herpetofaunal remains, it is hypothesized that paleoenvironmental interpretations can be enhanced through the use of paleoenvironmental indices and ternary diagrams that are based upon habitat preferences of modern amphibians and reptiles at the generic level for anurans and the subfamilial level for snakes.

Barboni *et al* (1999) used the ratio of ligneous dicotyledon (woody plants) to Poaceae (grass) phytoliths to estimate the amount of tree cover in Pleistocene paleoenvironments. In a similar fashion, an index of aquatic natricine snakes to colubrine snakes is calculated here to determine if sites have more of an upland or lowland influence. This is possible because modern natricine (water) snakes are generally restricted to permanent freshwater sources and colubrine snakes are found in drier upland sites. Similarly, bufonid toads are associated with dry upland areas away from permanent freshwater, hylid tree frogs are denizens of habitats that are near permanent water but they are not living in it or at its edge, and most ranid frogs, such as *Rana catesbeiana* (the bullfrog) and *Rana grylio* (the pig frog), are found in permanent freshwater environments (Conant and Collins, 1998). To quantify this, ranid, hylid, and bufonid percentages are plotted on a ternary diagram (Figure 4-1), with the apices representing, *Rana, Hyla,* and *Bufo.* The ternary

diagram (Figure 4-1) is split into four triangular sections that represent fully aquatic, fully terrestrial and partially aquatic environments, which can be used as a proxy to determine upland versus lowland sites.

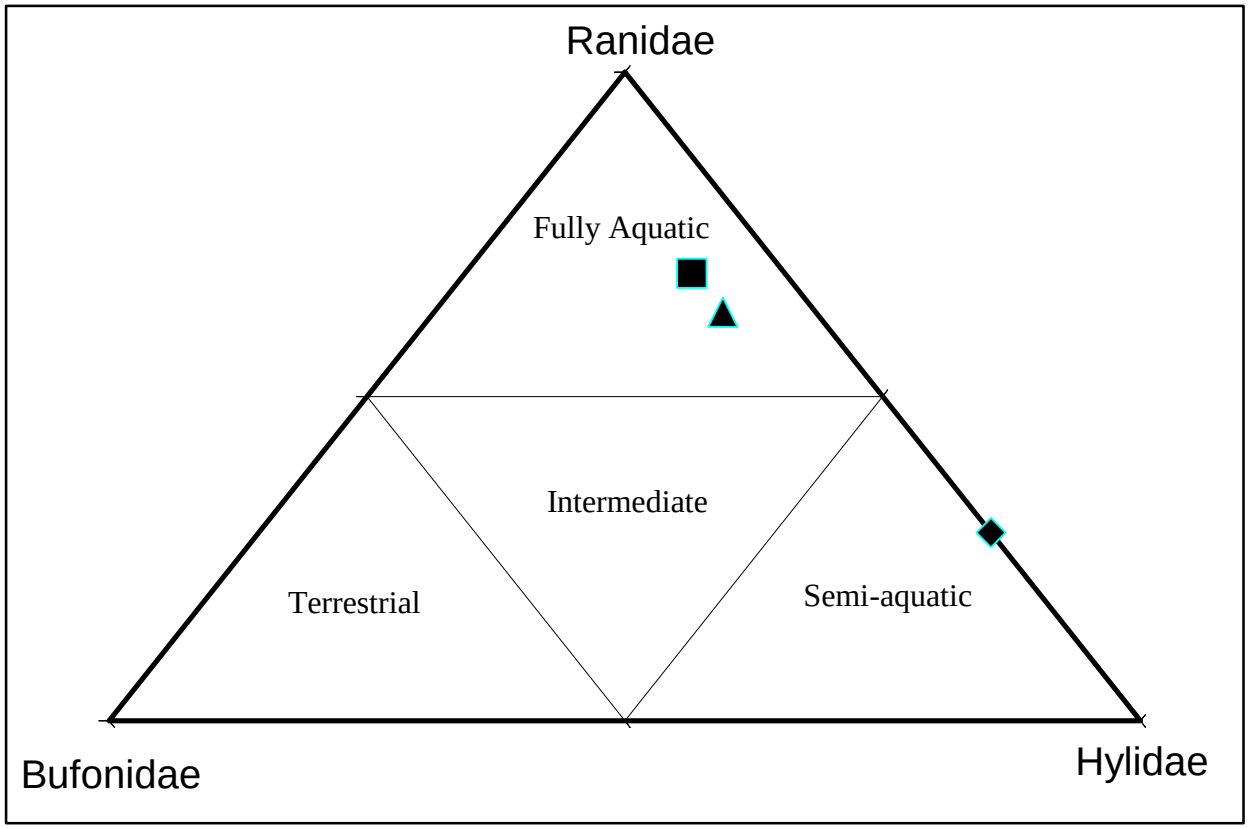

Figure 4-1. Ternary plot of Fort Polk frog data. The triangle represents total frog data for all Fort Polk sites. The square represents the Stonehenge site. The triangle represents the TVOR site.

It is hypothesized that calculating the number of identifiable herpetological elements per kg of matrix washed for the most prolific Fort Polk sites (Table 4-1), the use of natricine-colubrine indices, and plotting frog data on a ternary diagram, will be useful in distinguishing upland from lowland sites at the Fort Polk locality. The data used to calculate the indices and ternary diagram were derived from Table 4-2.

Table 4-1. Kilograms of sediment processed and yield of herpetofaunal elements for Fleming Formation sites on Fort Polk, western Louisiana. Yield refers to the number of identifiable amphibian and reptilian skeletal elements recovered through underwater sieving.

Collecting Site	Weight sediment processed (kg)	Yield	Yield/kg matrix
Stonehenge	3050.91	361	0.118
TVOR	2703.64	63	0.023
TVOR SE	1662.72	23	0.014
Discovery	1685.91	8	0.005
Gully	51.36	2	0.039
Total	**9154.54**	**457**	

Previous Paleoenvironmental Analyses for the Fort Polk Sites

Rodent abundances (Schiebout, 1997), palynological analyses (Schiebout, 1997), and mammalian size distribution (Schiebout and Ting, 2001) have all been used as paleoenvironmental proxies at the various Fort Polk sites. Comparing percentages of geomyoid, cricetid, and heteromyid rodents, Schiebout (1997) suggested that Stonehenge may have been more heavily forested than other Fort Polk sites, because of the abundance of cricetid rodents, which are known to frequent areas of denser tree cover than heteromyid rodents which prefer habitats with less tree cover.

The recovery of large amounts of fossil pollen from Fort Polk sites has allowed paleoenvironmental analyses to be conducted (Schiebout, 1997; Schiebout and Ting, 2002; Schiebout et al., 2002; Schiebout et al., 2004). There is no evidence of a marine influence in the palynological samples, and the most prolific samples imply a paleoenvironment consisting of both evergreen and deciduous forests (Schiebout and Ting, 2001). Fossil pollen has been sampled from TVOR, DISC 1, and DISC 2 cores and from the field at the TVOR, TVOR S, TVOR SE, and Discovery sites (Schiebout, 1997; Schiebout and Ting, 2001). The samples from the DISC I and DISC II cores did not contain abundant pollen grains, but what was recovered

indicated a terrestrial depositional environment with freshwater present on occasion (Schiebout, 1997; Schiebout and Ting, 2001).

Table 4-2. Total numbers of amphibian and reptile elements recovered from the Fort Polk sites. A, Stonehenge; B, TVOR; C, TVOR SE; D, TVOR North; E, TVOR North Creek; F, Discovery; G, Gully.

Taxon/Locality	A	B	C	D	E	F	G	**Total**
Siren miotexana	15	2	2	0	0	0	0	**19**
Siren, species	19	0	1	0	0	0	0	**20**
Notopthalmus slaughteri	4	0	0	0	0	0	0	**4**
Batrachosauroides	0	1	0	0	0	0	0	**1**
Salamander indeterminate	78	15	5	2	0	2	0	**102**
Acris sp.	7	3	0	0	1	0	0	**11**
Hyla miocenica	1	1	0	0	0	0	0	**2**
Hyla sp.	4	1	0	0	0	1	0	**6**
Rana sp.	38	3	1	0	0	1	0	**43**
Scaphiopus (*Spea*) sp.	2	0	0	0	0	0	0	**2**
Bufo cf. *Bufo hibbardi*	1	0	0	0	0	0	0	**1**
Bufo sp.	3	0	0	0	0	0	0	**3**
Anuran indeterminate	57	16	2	3	4	0	0	**82**
Trionychidae	0	0	0	0	0	1	0	**1**
Hesperotestudo sp.	0	0	0	0	0	2	0	**2**
Alligator sp.	0	1	0	0	0	0	0	**1**
Boavus cf. *Boavus affinis*	0	0	1	0	0	0	1	**2**
Boinae genus and sp. indeterminate	1	0	0	0	0	0	0	**1**
Calamagras sp. indeterminate	0	1	0	0	0	0	0	**1**
?*Ogmophis miocompactus*	5	2	0	0	0	0	0	**7**
Erycinae indeterminate	1	0	0	0	0	0	0	**1**
Boidae indeterminate	4	0	0	0	0	0	0	**4**
Ameiseophis cf *Ameiseophis robinsoni*	4	0	0	0	0	0	0	**4**
Salvadora cf. *Salvadora paleolineata*	2	1	1	0	0	0	0	**4**
Nebraskophis cf. Nebraskophis skinneri	2	0	0	0	0	0	0	**2**
Colubrine indeterminate	36	6	1	0	2	1	0	**46**
Neonatrix elongata	1	0	0	0	0	0	0	**1**
Neonatrix sp.	4	2	2	0	0	0	0	**8**
Natricine indeterminate	14	0	0	0	1	0	0	**15**
Viperidae	4	0	0	0	0	0	0	**4**
Ophidian indeterminate	54	8	7	0	4	0	1	**74**
Total	**361**	**63**	**23**	**5**	**12**	**8**	**2**	**474**

Although pollen grains were rare in the DISC conglomerate layers, the pollen collected was suggestive of terrestrial habitats (Schiebout, 1997; Schiebout and Ting, 2001). The TVOR conglomerate and TVOR core produced large numbers of pollen and fungal spores, indicative of a pine and hardwood forest, with a greater abundance of pine (Schiebout, 1997; Schiebout and Ting, 2001). Furthermore, the fungal spores suggested freshwater sources were present nearby (Schiebout, 1997; Schiebout and Ting, 2001). Pollen samples from TVOR S did not yield large numbers of palynomorphs, but indicated a coastal terrestrial setting that was occasionally wet (Schiebout, 1997). The pollen assemblage from TVOR SE was much like the assemblage from the TVOR core, with the exception of fungal spores, and represented a pine and hardwood forest (Schiebout and Ting, 2001; Schiebout *et al*, 2002).

Results

The Stonehenge site has the largest amount of sediment screened, greatest yield of identifiable elements, and the highest ratio of identifiable elements per kg of matrix (Table 4-1). The Discovery site has produced less herpetofaunal elements per kg of matrix washed than all other sites by at least one order of magnitude (Table 4-1; Figure 4-2).

Salamander vertebrae are the most common element from Fort Polk sites (Table 4-2; Figure 4-2). It is unfortunate; however, that the majority of the salamander vertebrae are not identifiable beyond salamander indeterminate because of the worn and abraded nature of the elements (Table 4-2). The Stonehenge and TVOR sites contain roughly equal numbers of frogs, snakes, and salamanders, while the TVOR Southeast site contains greater numbers of amphibian taxa than snakes (Table 4-2; Figure 4-2) Of the salamander taxa identifiable to genus or species, *Siren* is the most common, comprising 88% of the identifiable salamander vertebrae from all Fort Polk

sites and 90% of the taxa from the Stonehenge site. The abundance of *Siren* is followed by the newt, *Notopthalmus*, which only makes up 9% of identifiable taxa.

Anurans are common components of most Fort Polk sites (Table 4-2; Figure 4-2). Of the 68 anurans identified to genus and below for all Fort Polk sites, 63% are ranid, 28% are hylid, and 9% are bufonid+pelobatid (Table 4-2; Figure 4-2). The frog fauna from the Stonehenge site is comprised of 69% ranids, 22% hylids, and 9% bufonids; while the TVOR site is composed of 71% hylids and 29% ranids (Table 4-2; Figure 4-1).

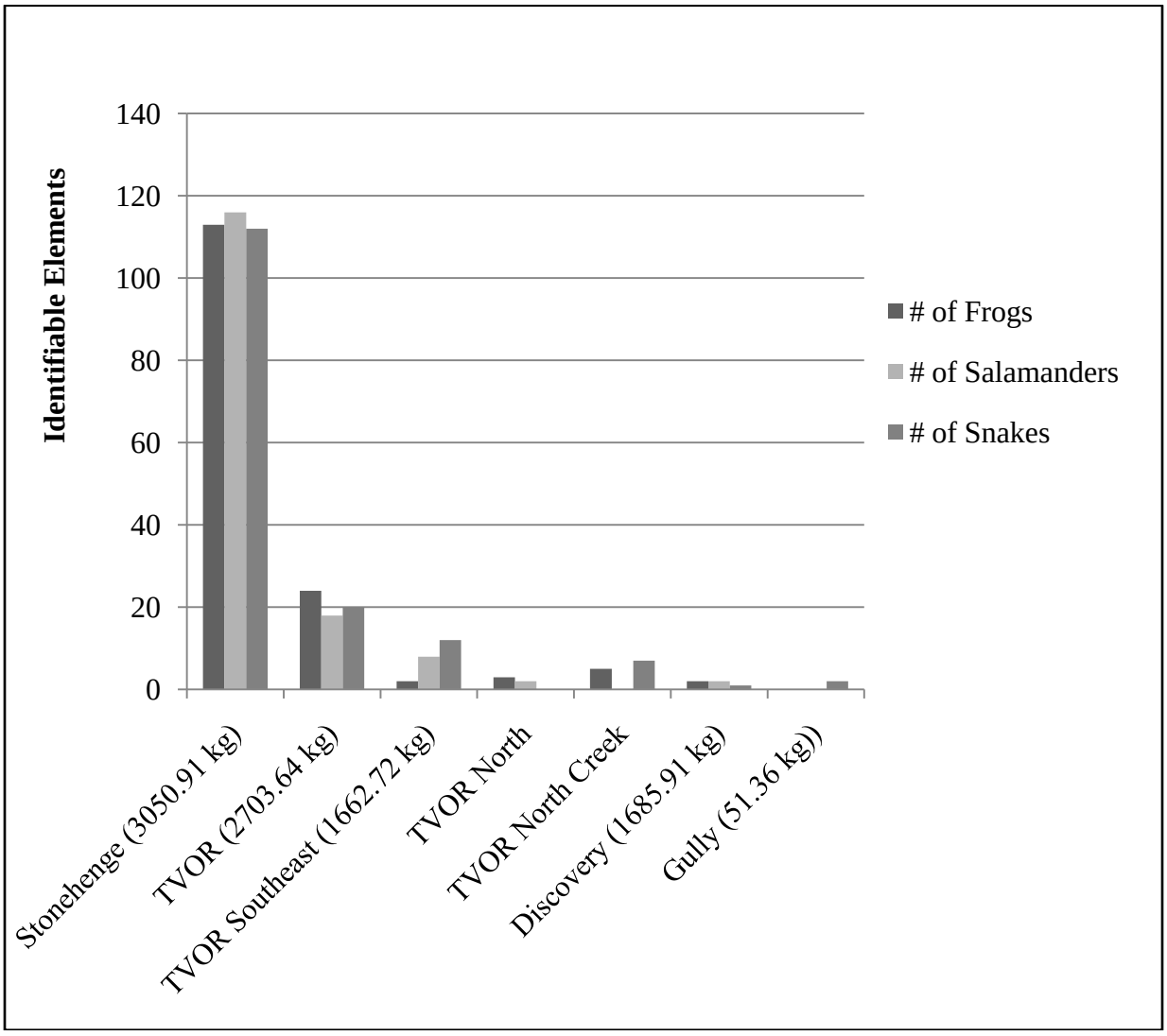

Figure 4-2. Total numbers of identified frog, salamander, and snake elements for Fort Polk sites.

The total number of colubrine snakes recovered from all Fort Polk sites is 56, and the natricine total number is 24, producing a natricine-colubrine index of 0.43. Considering the Stonehenge site alone, there are 44 colubrines and 19 natricines, which also is an index of 0.43. The TVOR site contains seven colubrines and 2 natricines, for an index of 0.29. Because the other Fort Polk sites have so few snakes, indices were not calculated.

Discussion

The number of aquatic taxa is considerable for all Fort Polk sites, especially Stonehenge. The abundant remains of *Rana*, and less abundant remains of *Acris*, *Hyla*, *Notophthalmus*, and *Siren* from the Stonehenge site imply a paleoenvironment with permanent water sources with very little to no current, such as bayous, swamps, and marshes. Ranid frogs would inhabit the water's edge, forests, or open grasslands very near the water. In general, ranid frogs are more closely tied to permanent water sources than are either hylids or bufonids. Modern *Acris* and *Hyla* live in forested to open grassy areas with permanent water in the near vicinity (Personal observation; Conant and Collins, 1998). *Notophthalmus* have three life stages, fully aquatic larval and adult stages and a terrestrial eft stage (Conant and Collins, 1998), so it is with some degree of caution that *Notophthalmus* is included as an aquatic taxon. *Siren*, on the other hand, is obligatorily aquatic (Conant and Collins, 1998).

Multiple proxies indicate the Discovery site as having the greatest upland influence of the Fort Polk sites. First, the low recovery rate per kilogram of matrix processed is suggestive of a more upland environment (Table 4-1; Figure 4-2), where fossil concentration through water transport was not as likely. Second, the abundant soil formed $CaCO_3$ nodules in the Discovery conglomerate are indicative of localized reworking of soils found in upland habitats (Schiebout, 1997; Schiebout and Ting, 2001). Finally, the presence of two nearly-complete, articulated

Hesperotestudo tortoise shells argues against much transport, and modern tortoises are not usually associated with habitats containing large amounts of standing water. Even with this evidence for a more upland environment at the Discovery site, it is interesting to note that of the few recovered herpetological specimens from the Discovery site, most hail from aquatic to semi-aquatic environments (Table 4-2). This is possibly due to localized reworking from a variety of habitats within coastal environments.

The ternary plot of Fort Polk frog data looks promising for quantifying paleoenvironmental determinations using fossil anurans. The plotted data (Figure 4-2) show the overall environment of Fort Polk to be an aquatic one, with the Stonehenge site to be the most aquatic site, which is in agreement with the number of herpetological elements recovered per kg of matrix (Table 4-1 and Figure 4-2). The environment was likely one in which there was year-round water such as bayous, swamps, and marshes. The frog fauna from the TVOR site indicate a paleoenvironment that was moist, possibly with seasonal water sources or permanent water nearby.

Natricine-colubrine indices are not indicative of localities with permanent water sources, as the number of natricine snakes compared to colubrids would be expected to be much higher. The indices do agree with the frog data, in that TVOR has a lower natricine-colubrine ratio than the Stonehenge site, suggesting a drier paleoenvironment.

Summary and Conclusions

- Based on the overall Fort Polk herpetofaunal composition, plotted frog data, natricine-colubrine indices, and the recovery rate for herpetofaunal elements, the Stonehenge site is the most aquatic terrestrial site, most likely a low-lying area with permanent water, such

as a swamp, bayou, or floodplain. TVOR site also had an aquatic influence, but to a lesser extent than Stonehenge. Seasonal rainfall may have created temporary pools.

- The plotted frog data separated the TVOR from the Stonehenge sites. Plotting frog data on ternary diagrams is a useful technique for separating upland from lowland sites, especially if large numbers of anuran material that are identifiable to the familial level are available.
- Natricine-colubrine paleoecological indices may not be as useful in sites where localized reworking of sediments has produced a fauna that may have come from multiple areas including upland and lowland. Even with the low numbers of natricines, however, the indices separated the Stonehenge and TVOR sites, and agreed with the frog data.
- The number of identifiable herpetological elements per kg of matrix washed also indicates Stonehenge to have more permanent water sources than TVOR. The Discovery site, which is the only site to have terrestrial tortoises, has the lowest yield of identifiable herpetological elements per kg of matrix washed and is the Fort Polk site with the greatest upland influence.
- The herpetological data agree with previous paleoenvironmental analyses, such as rodent percentages, which suggested Stonehenge to be the most heavily forested and may have represented a floodplain environment with water available year round.

CHAPTER 5: GLOBAL TRENDS IN MIOCENE OPHIDIAN ASSEMBLAGES

Introduction

The family Colubridae is a large (>1800 living species), cosmopolitan family of advanced snakes, which during the last approximately 35 million years, have spread to all continents of the globe, except Antarctica (Rage, 1988; Holman, 1995, 2000; Parmley and Holman, 1995; Pough et al, 2004). Not until the Late Oligocene to Early Miocene, more than ten million years after their origination, did colubrid snakes begin to diversify and become increasingly larger components of snake faunas (Rage, 1988; Parmley and Holman, 2003). The Paleogene history of the Colubridae is rather sparse, as snake faunas of this period are dominated by henophidian taxa, such as aniliid, boid, and paleopheid snakes (Parmley and Holman, 2003; Head et al., 2005). The earliest known colubrid snakes are a species of *Nebraskophis* from the Late Eocene (Chadronian NALMA) of central Georgia, USA (Parmley and Holman, 2003) and six vertebrae from the Late Eocene of Thailand (Rage et al., 1992) that were not identified below the familial level. Before the discovery of the Chadronian *Nebraskophis* from Georgia, the earliest colubrid snake from North America was the Early Oligocene (Orellan NAMLA) *Texasophis galbreathi,* discovered in eastern Colorado (Holman, 1984, 1999). In addition, Holman (1999) described *Floridaophis auffenbergi* and *Nebraskophis oligocenicus* from Early Oligocene (Whitneyan NALMA) sediments from north Florida.

During the Miocene, there was a gradual replacement of archaic henophidian snakes by more modern colubrid taxa, such that by the Late Miocene and Early Pliocene, henophidian snakes were rare elements of North American snake faunas (Holman, 1973; 1976a; 1979; 1996; 2000; Whistler and Wright, 1989; Parmley and Holman, 1995). Holman (2000) noted that Early Miocene colubrid taxa of North America were archaic; consisting of taxa like *Ameiseophis,*

Dakotaophis, *Paracoluber*, and *Texasophis*. These archaic colubrines were replaced by more modern taxa during the Late Miocene in North America.

Interestingly, a similar faunal turnover of European ophidian faunas, evidenced by a characteristic displacement of boids by colubrids in the Early to Middle Miocene, has been noted (Szyndlar and Scheich, 1993; Ivanov, 2000, 2001). In addition, Ivanov (2000) states that "Although representatives of Boidae are still common in West Europe by the lower/middle Miocene transition (Vieux Collonges), representatives of the Colubridae are predominant in Central Europe (Merkur, Dolnice, Petersbuch 2) already during the Early Miocene." Szyndlar and Schleich (1993) studied an astoundingly rich ophidian fauna consisting of over 4000 elements from the Early Miocene of Germany. This large and diverse fauna enabled them to document a significant replacement of archaic snakes by more modern immigrants, which they assumed probably arrived from the east (Szyndlar and Schleich, 1993).

Many authors have proposed Asia as the distributional center for colubrid snakes, with subsequent movements into Europe and North America (Rage, 1982, 1987, 1988; Rage and Holman, 1984; Rage et al., 1992; Holman, 2000; Holman and Harrison, 2001; Ivanov, 2001; Parmley and Holman, 2003; Head et al., 2005). Colubrid snakes first entered Europe from Asia in the Early Oligocene (Rage, 1988), and Oligocene to Miocene European ophidian faunas are known from Germany (Szyndlar et al., 1993), France (Ivanov, 2000 and 2001), Czech Republic (Ivanov 2002), and Poland (Mlynarski et al., 1982).

The question of what was driving the replacement of boids by colubrids during the Miocene of North America and Europe remains. Parmley and Holman (1995) suggested several possibilities for the North American cause. First, the rise of the Rocky Mountains changed the landscape from forested to grassland as the rain shadow effect strengthened in midwestern North

America. Second, passerine birds and rodents became more prevalent in North America during the Miocene, providing colubrid snakes with a new food source (Parmley and Holman, 1995). Third, they suggested the colonization of modern colubrids from Eurasia and the resulting struggle for resources was the impetus for the gradual dominance of colubrids over boids during the Miocene. The major ophidian faunal turnover during the Early to Middle Miocene of Europe has been attributed to the relatively warm Early Miocene conditions, compared to the cooler conditions, which dominated much of the Oligocene (Ivanov, 2000) or the Middle Miocene Climatic Optimum (MMCO) (Szyndlar and Scheich, 1993). However, this idea has not been proposed by North American workers and needs to be tested using the available fossil snake data from North America.

While any or all of the aforementioned factors is plausible and not discounted herein, I suggest that global climate was a major contributing factor in the spread of the Colubridae during the end of the Paleogene into the Neogene. With the exception of the extant erycine boas on the west coast of North America, *Lichanura trivirgata* and *Charina bottae*, modern boids live in tropical and subtropical environments and originated in the Late Cretaceous to the beginning of the Paleogene, a time when global temperatures were much greater than any time during the Miocene. The global climatic history, as displayed by the $\delta^{18}O$ record, of the end of the Paleogene into the Neogene attests to the global climatic alterations from cooler to hotter periods (Figure 5-1; Zachos *et al*., 2001). The Late Oligocene witnessed an abrupt warming trend after a relatively cool Early and Middle Oligocene. This warming trend was followed by cooling climate in the latest Oligocene, which continued until the MMCO approximately 17 mya (Zachos *et al.*, 2001). The MMCO was a warm period with average global temperatures not known since the Late Oligocene warming, 10 my prior (Zachos *et al*., 2002; Figure 5-1).

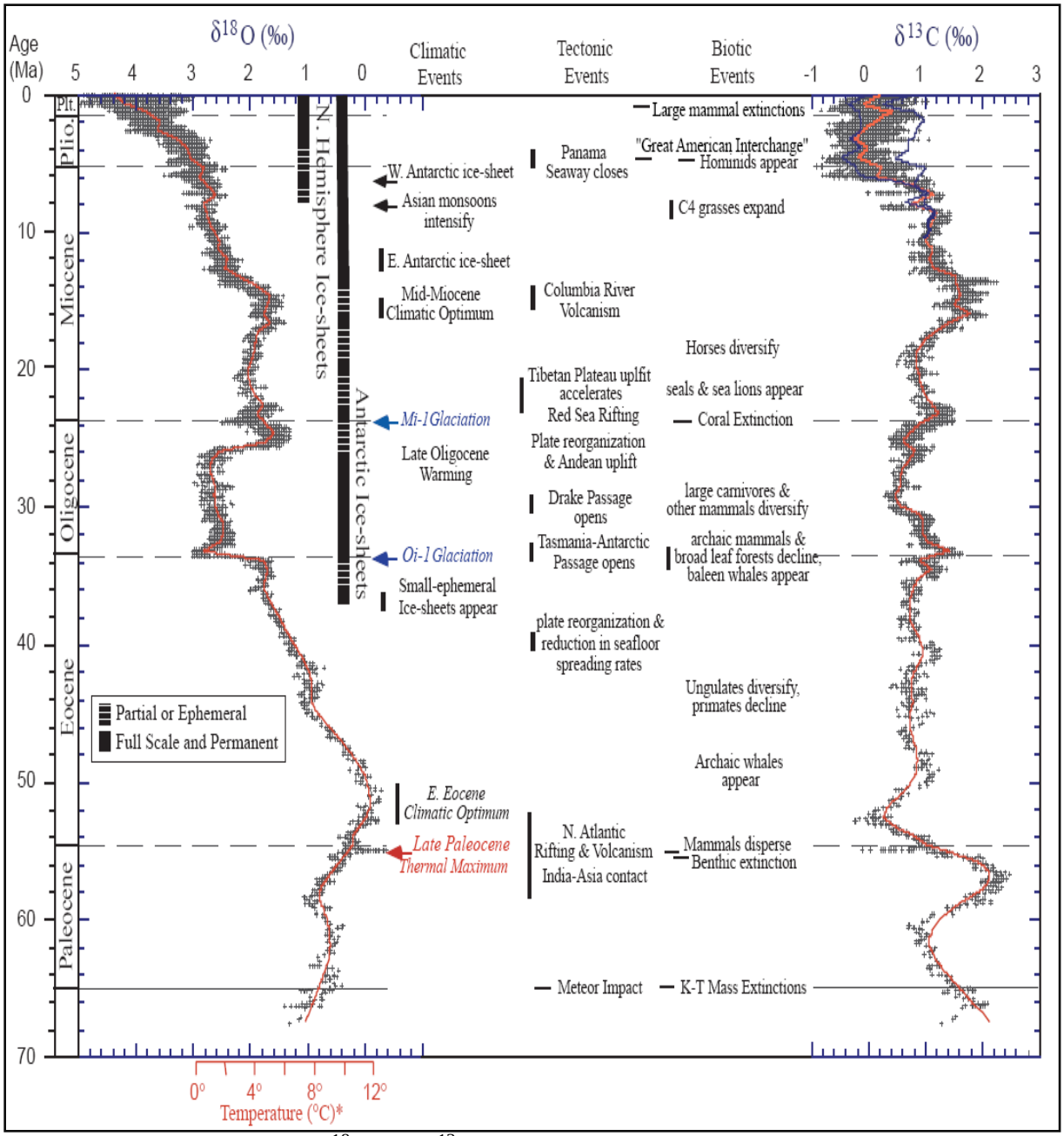

Figure 5-1. Graph of global $\delta^{18}O$ and $\delta^{13}C$ values for the Cenozoic, including pertinent climatic, tectonic, and biotic events. Modified from Zachos *et al*. (2001).

The MMCO was brief, only lasting a couple of million years, and was followed by a rapidly cooling climate, at a rate which had not been seen since the great cooling trend after the Early

Eocene Climatic Optimum, approximately 35 million years before (Figure 5-1; Zachos et al., 2002).

The purpose of this chapter is to determine if the spread of the Colubridae, during the Early to Middle Miocene in Europe and North America, can be related to global climatic alterations.

Methods

Fossil colubrid abundance data were compiled from North American and European Miocene ophidian faunas, with total numbers of colubrid snakes expressed as a percentage of the total number of colubrids and boids. These data were plotted as points at their corresponding ages, and the points were connected to create a curve in the same style as the $\delta^{18}O$ graph of Zachos et al. 2001 (Tables 5-1 and 5-2; Figure 33). The Fort Polk ophidian fauna were included in the dataset, because both colubrids and boids have been identified in the fauna. To minimize any biases attributable to small sample sizes, such as the Arikareean Harrison Formation locality, which has produced only one boid and one colubrid, comparably-aged samples were pooled to produce one data point. For instance, the percent colubrids from the sum of the total snakes from the two Oligocene localities Monroe Creek Formation, Wyoming (28-27 Ma), and Mouth of McCanns Canyon, Wyoming (27-26 Ma) were used to get the percent of colubrid snakes at 27 Ma, and the Early Miocene data point at 23 Ma is the colubrid percentage for the Toledo Bend Local Fauna, Texas (23 Ma), and the Harrison Formation, Nebraska (23-20 Ma) (Table 5-1). The Early Hemingfordian localities Black Bear Quarry II, South Dakota, and The Boron Local Fauna, California were summed to determine colubrid percentage at 19 Ma; the Hemingfordian Pollack Farm, Delaware and the Thomas Farm, Florida local faunas were the sources of the 18 Ma data point on Figure 5-2. The early Barstovian (~15.5 Ma) data point on figure 5-2 includes

the Moscow, Town Bluff, and Trinity River local faunas in Texas, and the Willacoochee Creek Fauna from Florida. The middle Barstovian (14.5 Ma) is represented by the Wood Mountain Formation, Canada, and the Egelhoff, and Norden Bridge local faunas of Nebraska. Late Barstovian localities plotted at 13 Ma include the Bijou Hills local fauna and Glenn Olson Quarry from South Dakota, the Myers Farm locality, Franklin County locality in Nebraska, and the Fort Polk herpetofauna. The Clarendonian data point at 10 Ma is from the Ricardo Formation, California, and the WaKeeney local fauna in Trego County, Kansas. The early Hemphillian (8 Ma) data come from the Higgins local fauna, and the late Hemphillian is represented by the White Cone local fauna, Arizona.

Results

North American colubrid abundances were close to zero in the Late Oligocene (Figure 5-2). Between 27 and 23 Ma, there was a significant increase in the percentage of colubrid snakes in Early Miocene ophidian faunas. This trend continued until approximately 19 Ma when colubrid abundance comprised 32% of total ophidian faunas (Figure 5-2). After 19 Ma, there was a major decline in colubrid abundance, as colubrid percentage dropped to 13% at 18 Ma. From 18 to 15.5 Ma, there was a significant increase in the numbers of colubrid snakes in the known ophidian faunas to 88%. The next million years was marked by a significant drop in colubrid percentages to 38% and was followed by a steady increase to 100% by 10 Ma. The period between 10 and 8 Ma saw a decrease of colubrid numbers to 83%, which was followed by an increase back to 100% by 6 Ma, after which no more fossil boids are known from any fossil locality in North America.

Table 5-1. Absolute numbers of Miocene North American colubrid and boid snakes

Locality	Age (Ma)	Reference	Colubrids	Boids+ Anilids	Colubrids+ Boids+ Aniliids	Percent Colubrid
Monroe Creek Fm, Wyoming	Arikareean (28-26)	Holman, 1977c	0	8	8	0%
Mouth of McCanns Canyon, Ne	Arikareean (27-26)	Holman, 1981	0	11	11	0%
Harrison Fm, Ne	Arikareean (23-20)	Holman, 1976c	1	1	2	50%
Toledo Bend LF, Tx	Arikareean (23)	Albright, 1991, 1994	0	6	6	0%
Black Bear Quarry II, S.D.	Early Hemingfordian (19-18)	Holman, 1976d	8	25	33	32%
Boron LF, Ca	Early Hemingfordian (18.5)	Whistler, 1984	6	3	9	67%
Pollack Farm, De	Hemingfordian (18)	Holman, 1998	2	3	5	40%
Thomas Farm, Fl	Hemingfordian (18-17)	Auffenberg, 1963	8	65	74	11%
Moscow LF, Tx	Early Barstovian (15.5)	Holman, 1977	9	1	10	90%
Trinity River LF, Tx	Early Barstovian (15.5)	Holman, 1966, 1991	9	2	11	82%
Willacoochee Creek Fauna, Fl	Early Barstovian (16-15.3)	Bryant 1991	3	0	3	100%
Living-stone Dam, Tx**	Barstovian (16)	Holman, 1977	0	1	1	0%
Town Bluff, Tx	Barstovian (16)	Holman, 1977	5	0	5	100%
Norden Bridge Local Fauna, Ne	Barstovian (14.5)	Holman, 1964	12	1	13	92%
Egelhoff Local Fauna, Ne	Barstovian (14.5)	Holman, 1973	54	3	57	95%
Wood Mountain Formation, Canada	Barstovian (14.5)	Holman, 1970	16	26 (one taxon)	42	38%
Bijou Hills LF, SD	Barstovian (13)	Holman, 1978	5	32	37	87%
Fort Polk	Barstovian (13.5)	Williams (This study)	80	16	96	83%
Myers Farm, Ne	Barstovian	Holman, 1977	426	191	617	69%
Franklin County, Ne	Barstovian (13)	Joeckel, 1988	5	4 (one taxon)	9	56%
Glenn Olson Quarry, SD	Late Barstovian	Green and Holman, 1977	3	1	4	75%
Ricardo Fauna, Ca	Early Late Clarendonian (10.0-10.1)	Whistler and Wright, 1989	37(One taxon)	0	37	100%
WaKeeney Local Fauna	Clarendonian	Holman, 1975	93	2	95	98%
Higgins Local Fauna, Tx	Early Hemphillian (8)	Parmley, 1988	6	1	7	86%
White Cone Local Fauna, Az	Late Hemphillian (6.5)	Parmley and Peck, 2002	15	0	15	100%

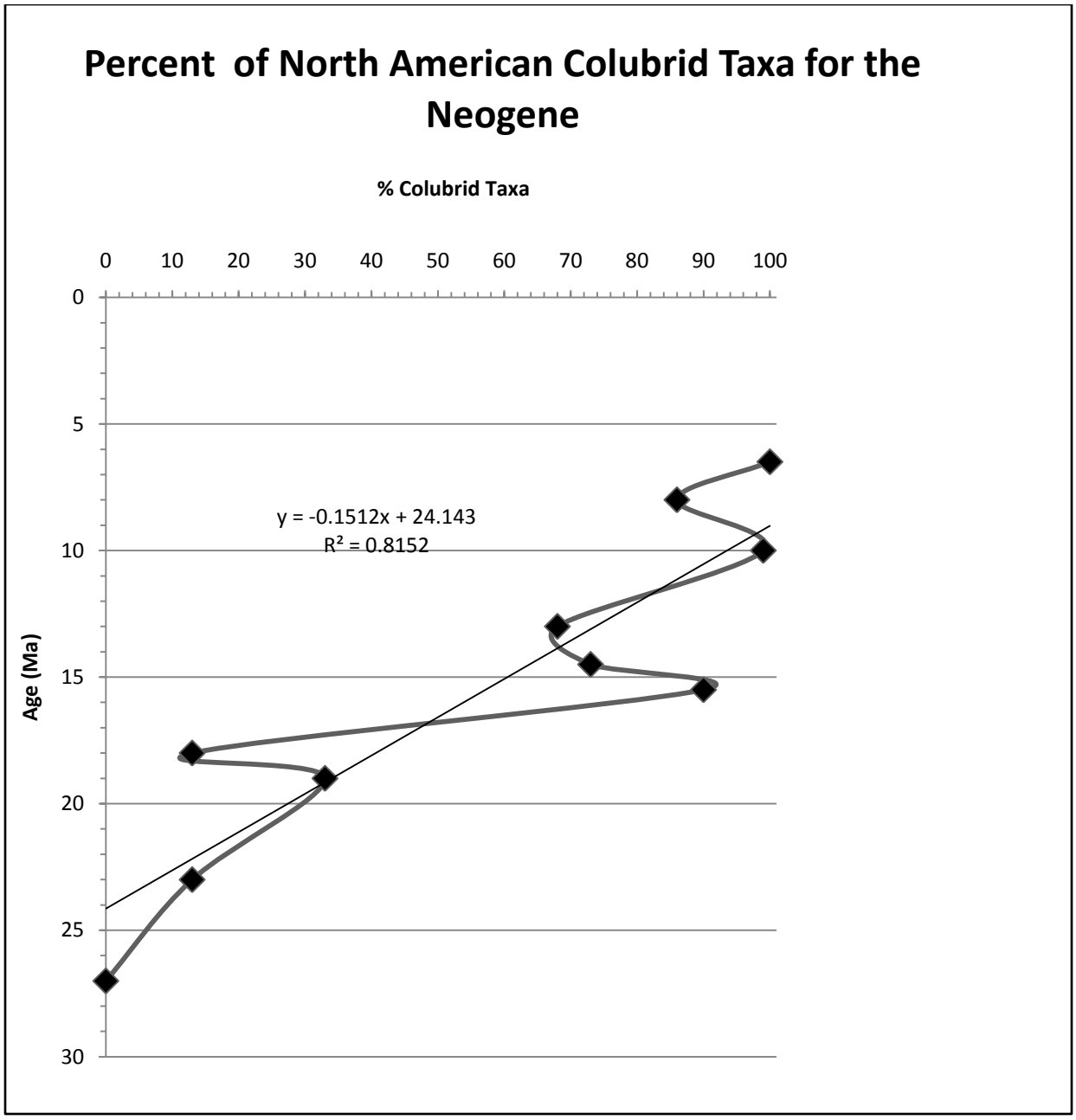

Figure 5-2. Scatterplot of North American late Paleogene to Neogene colubrid abundances as a percent of the total colubrid and boid fauna. The diamonds represent individual compiled data points.

The lack of European Neogene herpetofaunal data hampers the applicability of this technique at this time, although, an interesting trend is evident. Beginning approximately 20 Ma with the Merkur North locality in the Czech Republic, colubrid snakes comprised 98% of the ophidian

fauna (Figure 5-3; Table 5-2). European colubrid percentages decreased from 20 to 17 Ma; comprising 65% of the faunas 17 Ma and 18% at 16 Ma (Figure 5-3; Table 5-2). Following this was an increase to 23% at 12.5 Ma (Figure 5-3; Table 5-2).

Table 5-2. Absolute numbers colubrid and boid snakes from various European localities. *MN refers to the Mammal Neogene biochronological framework and dates in Millions of years (Agusti et al., 2001).

Locality	Age (Ma)	References	Total # of Colubrids	Total # of boids+ aniliids	Total # of Colubrids+ Boids+Aniliids	Colubrid Percentage
Merkur-North, Czech Republic	MN* 3a (~20)	Ivanov, 2002	711	14	725	98%
Dolnice, Czech Republic	MN 4 (17)	Szyndlar, 1987	103	20	123	84%
Petersbuch 2, Germany	MN 4 (17)	Szyndlar and Schleich, 1993	1375	756	2131	65%
Beon 1, France	MN 4 (17)	Rage, 2005	266	34	300	89%
Vieux Collonges	MN 4/5 (16.)	Ivanov, 2000	81	373	454	18%
NWK II, Opole, Poland	MN7 (12.5)	Mlynarski et al., 1982	6	20	26	23%

Discussion

The general trend of boids being replaced by colubrids during the Miocene of North America can be seen in Figure 5-2. Compared to the $\delta^{18}O$ curve of Zachos *et al* (2001), the beginning of an abrupt warming trend during the Late Oligocene corresponds with the start of the colubrid radiation (Figure 5-4). The first fluctuation of the snake data at approximately18 Ma is suspect, as the data come from the Thomas Farm locality in Florida, which displays a large degree of endemism, with two colubrid genera not found in other Hemingfordian localities in North

America (Auffenberg, 1963; Holman, 2000), and the Pollack Farm site in Delaware, which has a depauperate snake fauna with only five vertebrae identified in the fauna (Holman, 1998; 2000; Figures 5-2 and 5-4).

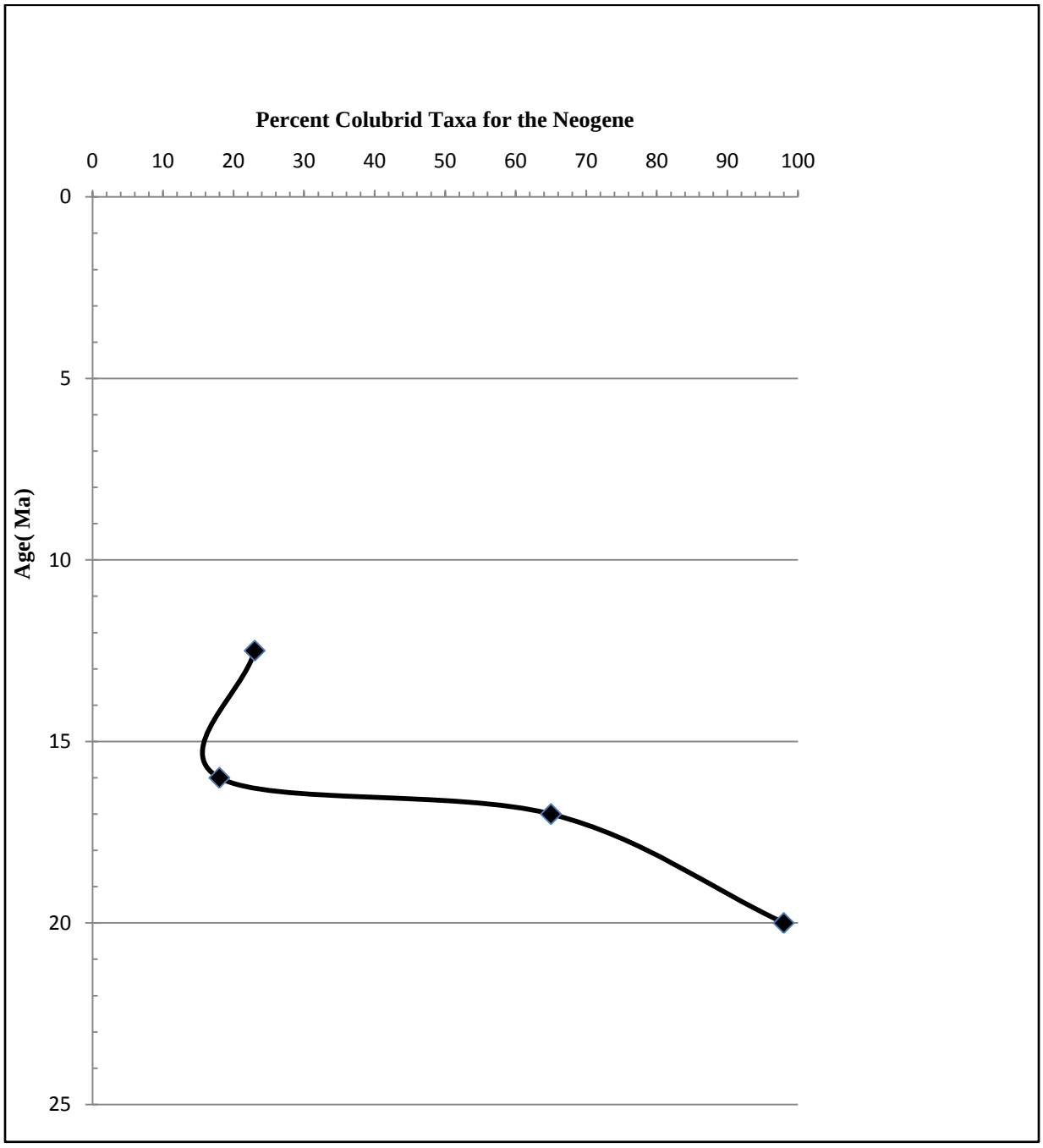

Figure 5-3. Scatterplot of European Neogene colubrid abundances as a percent of the total colubrid and boid fauna. The diamonds represent individual compiled data points.

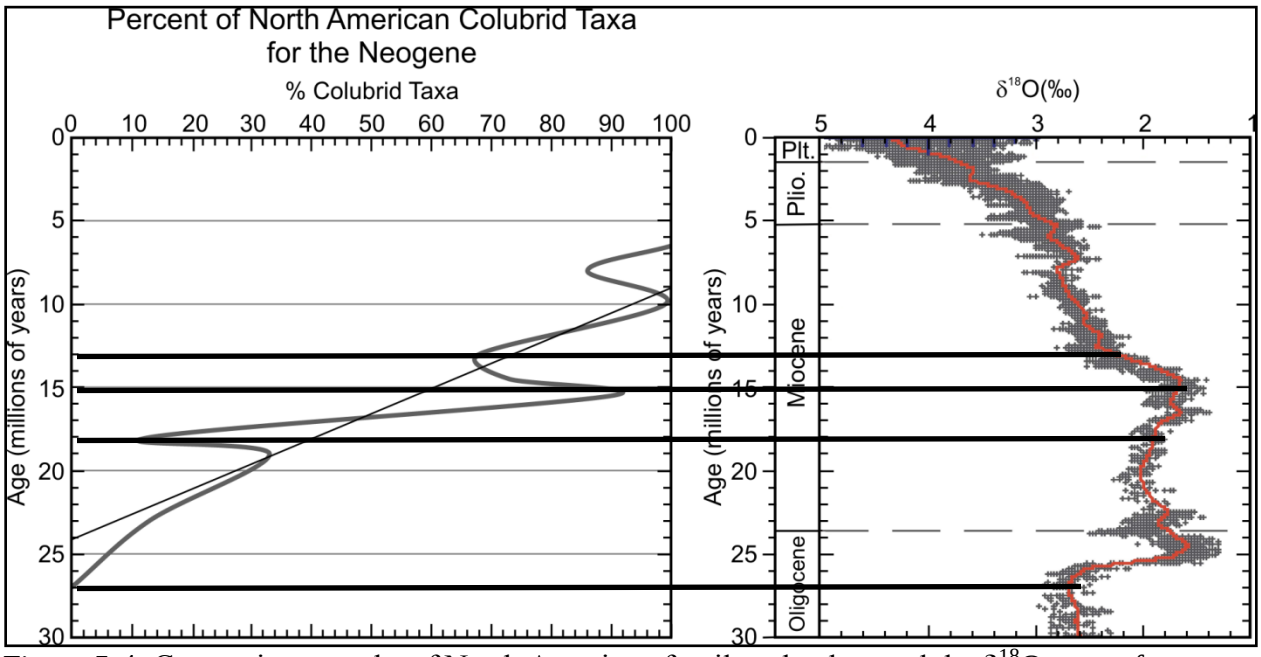

Figure 5-4. Comparison graphs of North American fossil snake data and the $\delta^{18}O$ proxy for global climate. Horizontal lines correlate significant events of the colubrid radiation with significant climatic events. $\delta^{18}O$ graph modified from Zachos *et al*., (2001).

These data may not be representative of the North American snake fauna at approximately 18 Ma. There is no evidence for major changes in global climate between 19 and 18 Ma that could account for such a fluctuation in North American snakes, other than the slight warming trend that began approximately 20 Ma and culminated in the MMCO (Figures 5-2 and 5-4; Zachos *et al*, 2001).

The large increase in North American colubrid snakes between 18 and approximately 15.5 Ma is noteworthy (Figure 5-4), as this period is within the increase in global temperatures seen in the $\delta^{18}O$ curve of Zachos *et al.* (2001), leading into the MMCO (Figure 5-4). Caution must be exercised because the early Barstovian data are only from the Gulf Coast of Texas and Florida, and may not reflect North American ophidian faunas as a whole.

A significant decrease in the numbers of North American colubrid snakes between 15.5 and

14.5 Ma can be seen in Figures 5-2 and 5-4. The decrease corresponds to the beginning of a decrease in global temperatures at the end of the MMCO. Once more, regional effects need to be considered; the middle Barstovian data point at 14.5 Ma is composed of data from localities in Saskatchewan, Canada, and Nebraska, both of which are northern localities (Table 5-1). Furthermore, the boid material from the Wood Mountain Formation in Saskatchewan, Canada, consists of 26 vertebrae from one taxon, causing a decrease in the percent colubrids in the fauna to 38% (Table 5-1). Whether the material represents one individual or many, cannot be determined.

Between 14.5 and 13 Ma, the decrease in proportions of colubrid snakes to boid snakes continued (Figures 5-2 and 5-4). The data come from South Dakota, Nebraska, and Louisiana. With the exception of the late Barstovian Franklin County site in Nebraska, which has four individuals of one taxon comprising the boid component of the fauna (56% colubrid), the percentages of colubrid taxa amongst the localities range from 87% in South Dakota, to 69% in Nebraska, with Fort Polk at 83% (Table 4). Compared to the $\delta^{18}O$ curve of Zachos *et al* (2001) (Figures 5-1 and 5-4), which displays a persistent cooling trend from 14.5 to 13 Ma, followed by a brief warming around 13 Ma, the snake data show a trend from a peak colubrid abundance at 15.5 Ma, decreasing to 68% colubrids at 13 Ma (Figures 5-2 and 5-4). After 13 Ma, colubrid abundance increases, as does the global temperature (Figures 5-2 and 5-4).

The increase in colubrid diversity from 68% colubrids at approximately 13 Ma to 99% colubrids at approximately 10 Ma is tenuous because the data come from the only two Clarendonian herpetofaunas known, the Ricardo fauna (Whistler and Wright, 1991) and the WaKeeney local fauna (Holman, 1975). The Ricardo fauna is one of a few Miocene herpetofaunas west of the Rocky Mountains and only contains 37 elements of one taxon

(Whistler and Wright, 1989), although there is more material from the locality awaiting study (David Whistler, Pers. Comm.). During the period between 13 and 10 Ma, there was a decrease in global climatic cooling rate compared to the previous couple of million years, punctuated by two slight increases in global temperatures (Figure 5-1).

Colubrid diversity decreased between 10 and 8 Ma from 99% to 86%, respectively (Figures 5-2 and 5-4). This decrease is only documented from one locality, the Higgins Local Fauna in Texas (Parmley, 1988; Table 4). During this period, global temperatures cooled at a relatively even rate, until approximately 8 Ma, when there was a rapid and short-lived increase in global temperatures, followed by a decrease in temperatures from approximately 7 to 6 Ma (Zachos *et al*., 2001; Figures 5-2 and 5-4). Based on data from the White Cone local fauna in Arizona (Parmley and Peck, 2002; Table 4), by the end of the cooling trend, North American colubrid abundances grew to 100% (Figures 5-2 and 5-4).

Miocene snake faunas from European localities display an opposite trend to those of North America. The data presented here echo that of Szyndlar and Scheich (1993) and Ivanov (2000, 2001) that the colubrid-boid transition took place in the Early Miocene. This is seen by the large proportion of colubrid snakes in the early Miocene. However, the decrease in colubrid snake diversity between 20 and 16 mya is unexpected. Unfortunately, this is based on limited data from only six localities.

Summary and Conclusions

While no overall direct correlation between decreasing temperatures and the spread of colubrid snakes in North America through the Miocene can be established, some notable trends are evident. First, large increases in the proportions of North American, Miocene colubrid snakes

occurred during times of increasing global temperatures. The colubrid radiation in North America began following a cool period in the Early Miocene, which coincided with the MI-1 glaciation event. Second, much of the faunal turnover in North America occurred between 18 and 15 Ma, approximating an increase in global temperatures leading up to the MMCO. Third, the decrease in colubrid taxa from 15.5 to 13 Ma coincided with the beginning of the cooling climate after the MMCO. Fourth, a decrease in the percent of North American colubrids between 10 and 8 Ma, occurred during a global cooling trend that ended abruptly at 8 Ma. Finally, North America colubrid abundances peaked at 100%, at approximately 6.5 Ma, which marked the end of another global cooling trend.

It is probable that localities with different depositional environments or localities that are far apart would contain different ratios of colubrid to boid snakes, but the correlations between changes in colubrid diversity through the Miocene of North America and major global switches in climate are suggestive. The discovery of more localities with abundant microfauna, such as the Hemphillian TunicaHills/Kerry locality in south Louisiana, will enhance this preliminary dataset.

While more limited than the North American data, the fossil snake data from Europe display a definitive trend that is opposite that of North America. Future work through the addition of more European faunas is necessary for more conclusions to be drawn.

CHAPTER 6: SUMMARY AND FINAL CONCLUSIONS

Compilation of previously-published fossil colubrid snake data from North America and Europe yields the following conclusions regarding the global spread of colubrid snakes and their use in biostratigraphy:

- In North America, colubrid diversity increased at the expense of boids beginning in the Early Miocene and rapidly radiated into the Middle Miocene, such that, by the early Barstovian, colubrid snakes were a larger component than boids of North American ophidian faunas.
- The spread of colubrid snakes in North America can be linked to global climatic events as seen on the global oxygen isotope curve of Zachos *et al* (2001). During the Late Oligocene, the beginning of the colubrid radiation corresponds to the Late Oligocene warming. The Middle Miocene of North America witnessed a major increase in proportions of colubrid snakes and is roughly equivalent to the MMCO.
- The increase in colubrid diversity occurred earlier in Europe, beginning in the Late Oligocene. By the Early Miocene, colubrids were dominant over boids, but decreased in abundance into the early Barstovian.
- Fossil snakes can be used to roughly subdivide the Miocene, but are not as useful as fossil mammals in terrestrial biostratigraphy because of longer stratigraphic ranges.
- Stratigraphic range plots of fossil snakes during the Miocene reveal possible extinction events at the end of the Barstovian and the late Hemphillian.

The Fort Polk herpetofauna is the only late Barstovian herpetofauna on the Gulf Coast, and the most diverse herpetofauna on the western and central Gulf Coast, with 15 genera in 10 families represented by approximately 474 elements. The extinct salamander, *Batrachosauroides*, was endemic to the Gulf Coast by the Miocene, as the geographic distribution was shrinking since the Eocene due to cooling climates and less abundant rainfall. The Fort Polk occurrence of this taxon is the stratigraphically youngest, and the Gulf Coast of North America was a refugium for *Batrachosauroides*. The presence of the snakes, *Ameiseophis robinsoni* and *Nebraskophis skinneri*, at Fort Polk represents a multi-state, southern increase in the geographic range of these taxa, making Fort Polk the southern extent of their geographic range. Overall, the herpetofaunas from the Great Plains and Gulf Coast share enough taxa to be considered one biogeographic province during the Middle Miocene.

The appearance of the toad, *Bufo hibbardi*, from multiple middle Barstovian localities in Nebraska implies an origination in the area at the time. Based on the early Barstovian east Texas record and the late Barstovian occurrence at Fort Polk, the boid snake, *Boavus affinis*, was a southern boid species arriving on the Gulf Coast from California by the early Barstovian. The snake, *Ogmophis miocompactus*, originated in the Great Plains during the Arikareean, and by the Barstovian, was no longer a major element of Great Plain's herpetofaunas because of either a change in paleoenvironment, being outcompeted by colubrid snakes, or both.

The Stonehenge site was the wettest Fort Polk site and probably represented a topographically low area with year around water. Ternary diagrams can be used to quantify paleoenvironmental determinations using fossil frogs if the locality has a large enough sample. Natricine-colubrine indices are not as powerful a proxy for paleoenvironmental reconstructions as frog data, although they can be useful, as they distinguished Stonehenge and TVOR sites.

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VITA

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